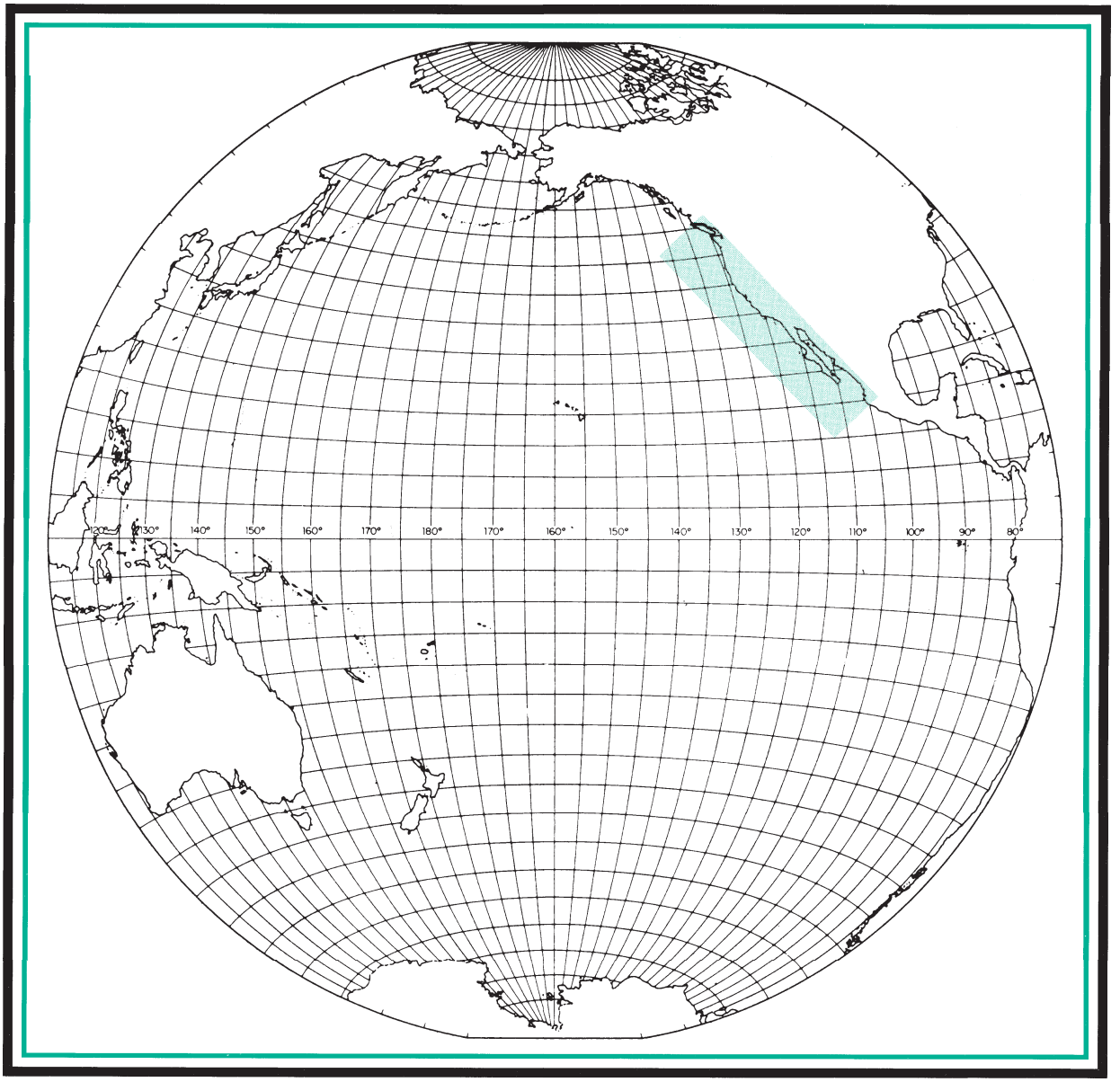

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Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE

NOAA HIGHLIGHTS

CalCOFI Cruises

The CalCOFI program completed its fifty-eighth year with four successful quarterly cruises. All four cruises were manned by personnel from both the NOAA Fisheries Southwest Fisheries Science Center (SWFSC) and Scripps Institution of Oceanography (SIO). The fall 2007 cruise was conducted on the SIO RV *New Horizon* and covered the southern lines of the CalCOFI pattern. The winter and spring 2007 cruises were conducted on the NOAA RV *David Starr Jordan*. The *Jordan* covered lines 93 to line 60 just north of San Francisco. The summer 2007 cruise was on the SIO RV *New Horizon*, and covered the standard CalCOFI pattern.

Standard CalCOFI protocols were followed during the four quarterly cruises. Over the year a total of 288 bongo tows, 266 manta tows, 212 pairovet tows, and 301 CTD casts were conducted. In addition to the usual CTD casts and net tows, measurements were collected on a variety of other parameters including, but not limited to, primary productivity, salinity, dissolved oxygen, acoustics, and weather. Both seabird and marine mammal observers also collected data on each cruise.

California Current Ecosystem Surveys

In 2008 the Fisheries Resources Division of the Southwest Fisheries Science Center plans on conducting two coast-wide California Current Ecosystem (CCE) Surveys. The first is scheduled to run 24 March–1 May 2008 using the NOAA RVs *David Starr Jordan* and *Miller Freeman*. The goals of the survey are to: (1) conduct continuous underway sampling of surface waters; (2) record current profiles throughout the duration of the cruise with the Acoustic Doppler Current Profiler; (3) continue an ongoing assessment of pelagic fish stocks between La Jolla and San Francisco, California; (4) collect information on sardine reproductive parameters, spatial distribution of size, age, and abundance of sardine, and acoustics ground truth information using trawling; (5) monitor environmental conditions within the CCE survey area; (6) make continuous observations of sea birds and marine mammals when possible; and (7) record continuous acoustic targets obtained with a multi-frequency Simrad EK-60 scientific sounder.

The *David Starr Jordan* will conduct operations in the Southern California Bight in San Diego and stations from Point Conception north to San Francisco, California. The *Miller Freeman* will synoptically conduct similar operations over the northern section of the CCE, in Port Townsend, Washington, and south to San Francisco. An additional California Current Ecosystem survey will be conducted in July 2008.

CalCOFI Ichthyoplankton Update

The SWFSC Ichthyoplankton Ecology group made progress on a multi-year project to update larval fish identifications to current standards from 1951 to the present, which will ultimately provide taxonomic consistency throughout the CalCOFI ichthyoplankton time series. The group updated samples collected during the first nine months of 1969 and from 1972 to the present. In addition, the group has begun re-identifying fish eggs collected in the CalCOFI bongo net samples, and is adding the count data for eggs of Pacific whiting (hake, *Merluccius productus*) and jack (*Trachurus symmetricus*) and Pacific mackerels (*Scomber australasicus*) to the database. Re-identifications have been completed for samples collected from 1992 to the present and the group will continue to work back through the time series.

During 2007 larval fish abundance continued to decline from the 2005 peak, to about 59% of the 2006 average abundance, and 30% of the 2005 average abundance. Northern anchovy (*Engraulis mordax*) larvae, the most abundant species collected in 2005 and 2006, declined precipitously in 2007 to about 16% of its 2006 abundance and 2% of its 2005 level. Pacific sardine (*Sardinops sagax*), on the other hand, increased in 2007 to about 15% above its 2006 abundance, although still well below its most recent peak (in 2005) of larval abundance. Ichthyoplankton data suggested that peak Pacific sardine spawning began to shift southward from central California in 2005, and this trend appears to have continued through 2007.

Review of Rockfish

SWFSC houses a collection of over 20,000 groundfish tissue samples, which includes virtually all extant rockfish species. These samples have enabled the completion of a comprehensive and robust phylogenetic hy-

pothesis for the genus *Sebastes* (Hyde and Vetter 2007). With at least 65 rockfish species found along the west coast of North America, this genus has presented numerous long-standing problems for identification and management. This work allowed: (1) major revisions to previous subgeneric classifications based on morphology; (2) assignment of approximate timing of speciation events; (3) evaluation of patterns of species evolution; and (4) the discovery of two "cryptic" species (Hyde and Vetter 2007; Hyde et al. 2008).

By using a combination of seven mitochondrial and two nuclear genes, the authors were able to develop a phylogeny of virtually all extant rockfish species including Asian, north Atlantic, and southern hemisphere forms. The results provide for the first time an unequivocal method of identifying ichthyoplankton and other field samples and forensic identification of market samples. An additional result is that rockfishes can now be assigned to meaningful sub-generic lineages that allow managers to group species under management according to shared life-history characteristics such as time of spawning and essential fish habitat requirements.

PaCOOS—Pacific Coast Ocean Observing System

In 2007 the focus for PaCOOS was to improve data access and interoperability and to develop new products for supporting the California Current (CC) ecological observing system. Data management activities centered on access of NOAA's West Coast biological and physical data in partnership with academics. With funds from the NOAA IOOS Program, three data portals were updated with QA/QC'd data and were made accessible from the PaCOOS website (www.pacoos.org) as well as through the following home servers:

1. NOAA Habitat data: http://tomcat.coas.oregonstate.edu/;
2. NOAA Pelagic data: http://oceanwatch.pfeg.noaa.gov/PaCOOS/; and
3. National Marine Sanctuary physical data: http://portal.ncddc.noaa.gov/wco/.

Through leveraging of PaCOOS funds with the CalCOFI and the California Current Ecosystem Long-Term Ecological Research (CCE LTER) Programs SIO, the historical CalCOFI physical and biological data are being made web accessible. The physical data are already available and the biological data will be available in 2008–09 (http://oceaninformatics.ucsd.edu/datazoo/).

Data access and data interoperability underlie the primary products of PaCOOS, ecological forecasts and assessments in the California Current. The recent closure of the California salmon fishery and the discussions at the Pacific Fisheries Management Council (PFMC) of how ocean conditions influence salmon demonstrate a growing need for ocean observing data and ecological forecasts.

Collaboration and partnerships within NOAA and between NOAA and academic scientists are the primary means of developing the next generation of ecosystem forecasts and assessments. Within NOAA, the Northwest Fisheries Science Center and SWFSC and the National Weather Service Climate Prediction Center are developing a pilot forecast to use wind field projections from existing atmospheric models in order to predict the timing and duration of the spring transition along the coasts of Washington, Oregon, and northern California. More information can be found at: http://www.cpc.ncep.noaa.gov/products/precip/CWlink/upwelling/mainupwelling.html. The SWFSC and SIO are developing a second ecological forecast with funds from the NOAA IOOS Program. This project utilizes existing SIO climate model outputs (temperature, salinity with depth, sea-surface height, and currents) to project West Coast Pacific sardine larvae distribution and abundance to improve NOAA Fisheries' annual coastal pelagic sardine stock assessment required by the PFMC.

The 2008 plans for PaCOOS include continued coordination with the Regional Associations on joint proposal development with an emphasis on data management, ecological forecasting and assessment, and increasing ocean observing data when opportunities arise.

CalCOFI Conference

The SWFSC Fisheries Resources Division hosted the CalCOFI Conference 26–28 November 2007 at Hubbs-SeaWorld Research Institute, San Diego, California. The symposium of the conference was "Jumbo squid invasions in the Eastern Pacific Ocean." The conference was well-attended with 130 participants from around the world.

As there were overlapping participants, the 8th Tri-National Sardine Forum was held immediately following the CalCOFI Conference, 29–30 November, also at Hubbs-SeaWorld Research Institute. The Forum provided an opportunity to exchange information regarding Pacific sardine issues among the fishing industry and scientists, government and academia from Mexico, the U.S., and Canada. The Forum was attended by 90 representatives from the SWFSC, NWFSC, PFMC, SIO, the States of California and Oregon, the Canadian Department of Fisheries and Oceans, the Ministry of Environment, Province of B.C., and several members from Mexico's CICESE and CICIMAR from Ensenada and La Paz. Industry was well represented from all three countries.

Other Surveys Conducted in the California Current

Lines 60 and 67 With NOAA funding, Monterey Bay Aquarium Research Institute (MBARI), National

Park Service (NPS), and University of California, Santa Cruz (UCSC) scientists continue to participate in CalCOFI shipboard occupations of Line 67 off Monterey and Line 60 off San Francisco, California. A suite of samples has consistently been collected quarterly along Line 67 since 1997. The focus has been on onshore/offshore and interannual variations, and the data document California Current and upwelling system dynamics over several El Niño-Southern Oscillation cycles as well as a probable shift in the Pacific Decadal Oscillation.

In 2007, MBARI and UCSC personnel collected nutrient, phytoplankton, and zooplankton samples during winter and spring cruises aboard the NOAA RV *David Starr Jordan* (lines 0701 and 0704). MBARI, NPS, and UCSC personnel conducted summer and fall cruises aboard the NOAA RVs *MacArthur II* (June) and *David Starr Jordan* (November). These data have been processed and quality-controlled, and are available both in the MBARI Biological Oceanography database and online. Briefly, 2007 was colder, saltier, and had higher chlorophyll concentrations than the mean. As analysis and publication proceed, the 2007 data should be especially interesting concerning: (a) the mid-latitude teleconnections and expression of the 2007–08 La Niña; and (b) the 2007 collapse of the northern and central California Chinook salmon (*Oncorhynchus tshawytscha*) fishery.

Trinidad Head Line An ocean observing effort (PaCOOS) has recently been established by NOAA Fisheries in cooperation with Humboldt State University. Data are collected at roughly monthly intervals along the Trinidad Head line, which consists of six stations along a transect extending approximately 27 nm due west from Trinidad Head. At each station, a CTD cast to 150 m (or as limited by bathymetry) is performed to collect data on temperature (T), salinity (S), dissolved oxygen (DO), fluorescence, and transmissivity, and plankton are sampled by: (1) an oblique tow from a maximum depth of 100 m with a 70 cm bongo frame fitted with dyed 505 µm and 335 µm mesh nets; and (2) a vertical haul of a PairoVET frame fitted with 153 µm mesh from a maximum depth of 70 m. Flowthrough instruments are used to sample near-surface T, S, fluorescence, and turbidity continuously along the ship's track. Since November 2007, all operations have been conducted at night. Cruises for which data are reported here are CS0704 (5 April), CS0706 (29 June), CS0711 (8–9 November), CS0712 (11–12 December), CS0802 (17–18 February), and CS0803 (5–6 March).

Observations along the Trinidad Head line (41°3.50'N) from spring 2007 through winter 2008 complement the regional patterns reported above, but also reflect the forcing by upwelling- or downwelling-favorable winds that immediately preceded each cruise and the variation in coastal freshwater input. Observations during spring 2007 captured a dominant signal of persistent upwelling, modified by a relaxation downwelling that coincided with sampling (CS0704). Conditions in June 2007 (CS0607) indicated relatively weak upwelling and mixing, and strong stratification in the upper 50 m along the entire transect. Conditions in November 2007 indicated the effects of persistent downwelling. In contrast, conditions during the 2007–08 winter and early spring were marked by shoaling of cooler, saltier water towards the coast. Both patterns are consistent with the trends in the monthly upwelling index between 39°N and 42°N.

COAST07 The SWFSC Advanced Survey Technology (AST) and In-Situ Survey groups have made operational a Collaborative Optically-Assisted Acoustic Survey Technique (COAST) to survey rockfish and evaluate their biotic and abiotic requirements for habitat. The COAST can provide estimates of biomass and dispersion by species throughout the Southern California Bight (SCB), with moderate sampling effort. The techniques were developed in 2003–04 on the Commercial Passenger Fishing Vessel (CPFV) *Outer Limits*, and were applied throughout the Southern California Bight (SCB) in 2004–05 and 2007 (COAST07), largely from the NOAA RV *David Starr Jordan*. The COAST will provide a time-series of data for improving rockfish stock assessments. Efforts are underway to also apply the COAST to rockfish off central California.

Throughout COAST07, acoustical volume backscattering strengths (Sv; dB re 1 m) and in-situ target strengths (TS; dB 1 m2) were measured continuously by four Simrad EK60 echo sounders configured with 38, 70, 120, and 200 kHz hull-mounted transducers. Then, video and high-resolution still images of the rockfish were collected using cameras deployed on a remotely operated vehicle (ROV). In each of 42 sites surveyed, a three-dimensional seafloor was visualized by interpolating the bottom detections from the 38 kHz echo sounder to render a surface. Empirical relationships between the multi-frequency Sv were used to remotely identify and separate the scatterer taxa (i.e., large fish, small fish, and zooplankton). Signals from the rockfish were thus extracted from the echograms and their distributions were overlaid on the rendering of the seafloor. Using these geographically-referenced files to navigate the ROV, optical images were obtained to characterize the fish species and their sizes, and also to validate acoustical seabed classifications. At the conclusion of each survey segment or day, a CTD was deployed in the area to profile the temperature, salinity, and sound speed within each survey location.

Additional optical surveys were conducted during December 2007 through April 2008, with the aid of partners in the sportfishing industry, to fill in missing data at a few sites. The goals were to examine the species

compositions and length distributions of bocaccio (*Sebastes paucispinis*), cowcod (*S. levis*), vermilion (*S. miniatus*), and bank rockfish (*S. rufus*) at all sites. Manuscripts detailing the methods and results of the COAST04/05 and COAST07 surveys are in preparation.

The AST and In-Situ Survey groups are currently analyzing the COAST07 survey data and planning surveys of the rockfish off Central California using the COAST. Tentative plans include COAST surveys of rockfishes around the Farallons and Cordell Bank. The groups are also working to improve COAST through better characterizations of habitat by species; quantification of the acoustic blind zone; improved length distributions by species; quantification of fish reactions to the ROV by species; improved models of TS by species, length, depth, and frequency; and quantification of total survey error by species.

Shark Surveys The SWFSC's shark research group collects data to support the management of blue (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), and common thresher sharks (*Alopias vulpinus*), all of which are common in the Southern California Bight and taken in regional fisheries, primarily as juveniles. Common thresher and mako sharks have the greatest commercial value and are also targeted by sport fishers. Although the blue shark has little market importance in the United States, it is a leading bycatch species in a number of U.S. fisheries and is targeted in Mexico. One of the primary methods used to collect data on the three species are fisheries-independent surveys. These surveys provide catch data that allow trends in abundance to be tracked. Use of fisheries data alone for estimating population status is complicated by changes in regulations, fishing methods, and areas over time. The surveys also provide the opportunity to deploy conventional and electronic tags, obtain biological samples, and conduct studies on age and growth.

In June and July of 2007, the SWFSC conducted its fourteenth juvenile shark survey since 1994. Working aboard the NOAA RV *David Starr Jordan*, a total of 5,759 hooks at 28 sampling stations in seven main areas in the Southern California Bight were fished. The survey catch totaled 112 makos, 139 blue sharks, 14 pelagic rays (*Pteroplatytrygon violacea*), and 1 ocean sunfish (*Mola mola*). Of these, 12 mako sharks, 4 blue sharks, and the sunfish were tagged with satellite tags and most were conventionally tagged and injected with oxytetracycline (OTC). From catch data, the index of relative abundance for juvenile sharks, defined as catch per 100 hook hours, was calculated for seven target survey areas. The overall survey catch rate was 0.556 per 100 hook hours for mako and 0.666 per 100 hook hours for blue sharks. The CPUE for mako sharks has increased slightly since 2003, however, there is a declining trend in CPUE for both species over the time series of the survey.

In September of 2007, the SWFSC team worked with the CPFV *Outer Banks* to sample common thresher sharks in the California Bight from Point Conception to the Mexico border. Forty-nine longline sets were made in relatively shallow nearshore waters. Over the 18-day cruise, 137 common thresher sharks, 2 shovelnose guitarfish (*Rhinobatos productus*), 2 soupfin sharks (*Galeorhinus galeus*), 1 leopard shark (*Triakis semifasciata*), and 1 bat ray (*Myliobatis californica*) were caught. Roughly 65% of the threshers caught were young-of-the-year (<100 cm FL). Nearly all of the threshers caught were injected with OTC for age and growth studies, tagged with conventional tags, and released. In addition, satellite tags were deployed on four thresher sharks.

Ocean Salmon Ecology A cruise was conducted on the NOAA RV *David Starr Jordan* (DS-07-05) 10–20 August 2007 to investigate the ocean ecology of juvenile salmon. The objectives of the cruise were to: (1) determine the growth, feeding, energy status, and spatial distribution of juvenile salmonids in the coastal ocean off northern California and southern Oregon; (2) analyze the relationship between oceanographic conditions and features and salmon dynamics; (3) quantify and describe the coastal pelagic fish and macroinvertebrate community; and (4) collect jumbo squid, *Dosidicus gigas*, for trophic analysis. Trawl stations were located between the Golden Gate and Cape Blanco in 50 m to 150 m water depths. At each trawl station a suite of operations were conducted, including a CTD cast to record temperature, salinity, chlorophyll fluorescence, photosynthetically available radiation, and transmissivity; water samples by Niskin bottle at 1 m and the chlorophyll maximum depth for discrete chlorophyll analysis; an oblique Bongo net tow to collect zooplankton; a Manta net tow to collect neuston, and a 20–30 min tow with a 264 Nordic rope trawl fished at the surface at 3–4 knots. All stations were trawled during daylight. Horizontal temperature, salinity, and chlorophyll concentrations were recorded continuously, day and night, with a SCS thermosalinometer and a Turner SCUFA fluorometer. At night, CTD drops were performed in a grid design to cover the shelf area where trawls were conducted. Also, during the night at deep stations (>200 m) hook-and-line fishing for jumbo squid was performed. In all, 29 trawl stations and 87 CTD stations were completed.

At 3 m depth, temperature ranged from 9.6°C to 18.5°C with highest temperatures on the southern Oregon coast. Salinity varied little during the cruise, ranging from 32.74 psu to 33.96 psu. Surface chlorophyll was highest in the Gulf of the Farallones and lowest between Point Reyes and Cape Mendocino.

A total of 110 juvenile salmon and 15 adults were captured in 29 trawl sets. The majority were caught in a few sets between Cape Mendocino and Trinidad

Head. Preliminary analysis indicates most of the juvenile salmon were coho based on pyloric caecae counts, but the discrimination between coho (*Oncorhynchus kisutch*) and Chinook juveniles at this stage (~200–300 mm fork length) is difficult. Final species counts await genetic analysis. Twenty-one juvenile steelhead (*Oncorhynchus mykiss*) were also collected, as were 27 jumbo squid.

West Coast Midwater Trawl Survey The seventh annual West Coast midwater trawl survey was completed in 2007 from 4 May–17 June. This coast-wide survey represents a major geographical expansion of the SWFSC Fisheries Ecology Division's pelagic juvenile rockfish survey, which historically was fielded in the central California region between Carmel and Bodega Bay. Now the survey spans the entire U.S. west coast and in 2007 extended from San Diego, California (lat. 32°42'N), to Cape Alava, Washington (lat. 48°06'N). The expansion of the survey has been accomplished by a latitudinal extension of trawling by the NOAA RV *David Starr Jordan* to encompass the region between San Diego and Point Delgada (lat. 40°00'N), and by coordination with the NWFSC's pre-recruit Pacific whiting midwater trawl survey aboard the FV *Excalibur*, which samples from Monterey (lat. 36°30'N) to Cape Alava. In 2007 the two vessels completed a total of 182 and 152 midwater trawls, respectively, including 21 paired trawls wherein the ships sampled side-by-side to calibrate the two surveys. The NWFSC survey has been conducted cooperatively with the Pacific Whiting Conservation Cooperative since 2001. In addition to the biological data collected during the combined survey, a variety of physical data were gathered aboard the *David Starr Jordan*, including 268 CTD casts (with fluorometry) and continuous underway sampling of temperature, salinity, fluorescence, ADCP, and hydroacoustic data.

In 2007 the coast-wide abundance of young-of-the-year (YOY) rockfish (*Sebastes* spp.) was quite low (13 fish/trawl), being well below the 2001–07 long-term mean of 25 fish/trawl. Only squarespot rockfish (*S. hopkinsi*) was encountered in above average quantities and catches of that species were limited in its distribution to the Southern California Bight. Abundances of young-of-the-year hake were also down and, other than a single large tow at San Clemente Island, were largely limited in their distribution to the region between Monterey Bay and Cape Mendocino.

SIO HIGHLIGHTS

Scripps Institution of Oceanography participated on all four CalCOFI cruises. While the spring and summer cruises suffered from rough weather and some stations were not surveyed, these cruises were a success overall. The ISUS nitrate sensor, mounted on the CTD, has by now become an integral part of the system and produces reliable data; these, however, do not match the accuracy of those generated using chemical analyses for nitrate. The CCE-LTER group participated on all four cruises and augmented CalCOFI sampling with measurements aimed at characterizing biogeochemical cycling and lower trophic-level community structure in more detail. The marine mammal program participated on all four cruises as well, using visual observers and acoustic methods to enumerate the abundance of marine mammals on stations and along the cruise tracks. The seabird program, due to funding restrictions, was not able to participate on all cruises; however the important ones for that program, winter (January) and summer (July), were covered in 2007.

Observations made over the last year showed that the basin-wide La Niña conditions significantly affected the California Current System. Southward coastal winds were anomalously strong and, as a consequence, upwelling was stronger than normal. Mixed-layer temperatures and nutricline depths were below long-term averages and mixed-layer concentrations of nitrate were elevated during the last year. However, concentrations of chlorophyll *a* and rates of primary production were not significantly affected by these changes in water-column structure and chemistry. Zooplankton displacement volumes were similar to values observed during previous years. The discrepancy between changes in water-column structure and chemistry and biological responses may well be due to differential responses of different areas of our study domain, a topic we are pursuing currently.

The most important results for the seabird program include the following climate-change-related observations: (1) continuing low abundance, in comparison with the late 1980s and early 1990s, of trans-hemispheric migrants in the California Current including Sooty (and some Short-tailed, *Puffinus tenuirostris*) Shearwaters (*Puffinus griseus*); and (2) a recent and continuing increase in the at-sea abundance of Cassin's Auklet (*Ptychoramphus aleuticus*), an obligate krill-feeding planktivore, which started in July of 2005 and persisted in July 2006 and July 2007.

Ashore-data processing progresses on schedule. We have begun to make the CTD data publicly available and have reprocessed these for past cruises. We began to use CTD data instead of interpolated data at standard levels, thus increasing the accuracy of the interpolations. We are now in the process of merging CalCOFI hydrographic data and CCE-LTER data, using the DataZoo software developed by the CCE-LTER group.

The Gordon and Betty Moore Foundation funded a joint SIO-SWFSC project to develop an acoustics capacity for future CalCOFI cruises and related studies of

the California Current ecosystem. A five-frequency (18, 38, 70, 120, and 200 kHz) Simrad EK-60 system was purchased and hull-mounted on the RV *New Horizon* in May 2008. A portable pole-mounted four-frequency (38, 70, 120, and 200 kHz) system will be fabricated for use on other vessels. The first anticipated deployment of the portable system will be on the CCE-LTER cruise in October 2008, when it will be used to assess the distribution and biomass of the midwater micro-nekton and its role in carbon sequestration in the California Current, a study led by an SIO Ph.D. candidate. A single-warp, Japanese-designed midwater trawl with a 5 m^2 mouth opening is being built to ground-truth the acoustics, and funds are being requested for two additional sea days on Scripps' CalCOFI cruises in 2009 to utilize the new acoustic and trawl sampling capability. The aim of this new sampling will be to examine the ecology of mid to higher trophic levels in the California Current, as the basis for ecosystem-based fishery management. Specific objectives are to assess the biomass and distribution of micro-nekton, krill, juvenile, and forage fishes in relation to hydrographic features in the California Current, and to sample and assess the ecology of the late larvae and juveniles of key fish species in relation to oceanographic conditions.

Funding was received from the California Coastal Conservancy in March 2008 for a two-year project. The project has four objectives: (1) to describe the ichthyoplankton assemblages of nearshore coastal habitats, based on recent and historical CalCOFI samples and past nearshore ichthyoplankton studies; (2) to develop indices of stock size and recruitment for the California spiny lobster (*Panulirus interruptus*), based on phyllosoma abundance from historical CalCOFI samples; (3) to assess the potential impacts of climate variability and climate change on the phyllosoma; and (4) to develop a central, publicly available database for the CalCOFI program, combining available ichthyoplankton, larval invertebrate, and hydrographic data held at SIO and the SWFSC.

Scientists from SIO, Oregon State University, the SWFSC and NWFSC, and other institutions jointly submitted a proposal to a new NSF/NOAA funded program for the Comparative Analysis of Marine Ecosystem Organization (CAMEO). If funded, the project will compare ecosystem organization and the response to climate forcing in the northern and southern California Current, focusing on krill and the recruitment dynamics of sardine, anchovy, and hake. The project would bring together time series, including CalCOFI, from northern and southern sectors of the California Current, initiate pilot field studies that would build on CalCOFI and other regional time-series studies, and develop biophysical modeling of the region, with the aim of enhancing ecosystem-based management of key fisheries.

CDFG HIGHLIGHTS

Marine Regulatory Changes

The Fish and Game Commission adopted significant changes to its mandatory reporting and tagging programs for recreational fishermen late in 2007. Beginning in 2008, report cards are required for all fishermen, including children, pier fisherman, and on free fishing days. Report cards serve to provide information on catch and fishing activity (effort), and improve compliance with existing bag limits and other rules. For species of high commercial value, report cards can also help reduce the potential for illegal take and commercialization. The California Department of Fish and Game (the Department or CDFG) has report card requirements only for species of particular importance or concern. Before the new regulations were adopted, report cards were required for steelhead, salmon, sturgeon, and abalone fishing. The new regulations add a card requirement for spiny lobster, and a requirement that any abalone taken in the recreational fishery must be tagged and recorded on the card.

For the first time, the Pacific Fishery Management Council recommended regulations to constrain recreational tuna fishing off California, in response to declines in stocks. NOAA Fisheries adopted a bag limit of 10 albacore (*Thunnus alalunga*) for federal waters south of a line drawn at Point Conception, and a 25-fish bag limit for waters north of that line. The Fish and Game Commission adopted similar rules for state waters.

CDFG Marine Region staff assisted the Department's Oil Spill Response Program in the assessments of the impact of the container ship MV *Cosco Busan* oil spill. A spill on 8 November 2007 in San Francisco Bay resulted in a temporary closure of recreational and commercial fisheries within the bay and from Point Reyes Light south to San Pedro Point. To determine the health risks of consuming bay-area marine life, CDFG Marine Region staff collected close to 1,000 crabs, mussels, herring, and surfperch from a variety of locations and depths both inside and outside the spill zone for laboratory testing. Testing results showed that fish and shellfish (with the exception of mussels found in two bay locations) from the spill area were safe to eat. Therefore, San Francisco Bay-area fisheries were reopened on 29 November 2007. A natural resources damage assessment study will be conducted during the 2007–08 herring (*Clupea pallasii*) spawning season within the bay to determine if lingering contaminants from the spill are negatively impacting herring eggs and larvae. For more information go to http://www.dfg.ca.gov/ospr/spill/incidents/cosco_busan/cosco_busan.html in Nov. 2007.

Aquaculture and Bay Management

The Aquaculture and Bay Management Project (ABMP) completed the California Pacific Herring Commercial Fishing Regulations Supplemental Environmental Document (SED) for the 2007–08 season. The SED included the herring spawning biomass estimates, spawning population, and commercial catch assessment. In addition, the SED included the results of sub-aquatic vegetation surveys in key herring spawning areas for San Francisco Bay for the 2006–07 season. The spawning biomass estimate for San Francisco Bay of 10,935 tons (including catch) for the 2006–07 season is the lowest recorded estimate in the history of the roe herring fishery (1978–79 to present) and a 92% decrease over last season's estimate of 145,054 tons.

Invertebrate Fisheries

The Invertebrate Project added several new staff in 2007, allowing an increase in resource assessment capabilities. A lobster team was created and has embarked on several assessment efforts including a sport lobster trap efficiency comparison study and a night-time sport lobster creel survey. Red abalone (*Haliotis rufescens*) recruitment and aggregation indices are being developed. In northern California, new staff have begun assessing Dungeness crab (*Cancer magister*) megalopae abundances in light traps in Bodega and Humboldt Bays. In addition, surveys began in 2007 of recreational clammers on Humboldt Bay and Clam Beach in Humboldt County to continue collecting historic catch and effort data. In southern California, cooperative abalone stock assessments were conducted for the second year around San Miguel Island using fishing industry divers trained in dive transect techniques as well as Department and Kelp Forest Monitoring divers. Furthermore, there is a process underway examining the potential for a fishery of red abalone at San Miguel Island.

Groundfish Highlights

In 2007, management measures for state and federally managed groundfish species were similar to 2006 in California recreational and commercial fisheries, with a few exceptions. In September, the California Fish and Game Commission took emergency action to conform state regulations to match federal action that closed the recreational fishery in the Northern and North-Central Management Areas on 1 October; this action was taken due to higher-than-expected catches of canary (*Sebastes pinniger*) and yelloweye (*Sebastes ruberrimus*) rockfish, both federally-designated "overfished" species. Commercial fisheries for California sheephead (*Semicossyphus pulcher*) and greenling (*Hexxagrammos* spp.) were closed early due to concerns that allocations would be exceeded. In addition, cabezon (*Scorpaenichthys marmoratus*) trip limits were lowered in the fall to maintain the season through the end of the year.

A new stock assessment of blue rockfish (*Sebastes mystinus*) was conducted in California waters and it was not determined to be "overfished" as defined by the Nearshore Fishery Management Plan. The stock's biomass was estimated to be above the "overfished" threshold of 30% but below 50% of the unfished biomass. The results of this assessment will be used to develop nearshore fishery regulations for the 2009–10 management season.

Recreational Fisheries

The California Recreational Fisheries Survey (CRFS) began in January 2004 to provide catch and effort estimates for marine recreational finfish fisheries. This is the updated version of the marine recreational finfish fisheries statistical survey (MRFSS) which started in 1980. The CRFS generates monthly estimates of total recreational catch for four modes of fishing (beach/bank and shore, piers and jetties, commercial passenger fishing vessels, and private vessels launched from public launch ramps) for six geographic districts along California's 1,000 plus miles of coast. These data are used by state and federal regulators to craft regulations protecting fish stocks and provide recreational fishing opportunities.

The CRFS includes field sampling and telephone surveys. In 2007, approximately 45 samplers worked to gather the field data. The CRFS samplers interviewed more than 98,000 anglers at 414 sites, and examined almost 194,000 fish. The licensed angler telephone survey completed almost 26,000 interviews in 2007 which is comparable to the number completed in 2006.

A review of the first three years of CRFS data was undertaken in 2007 to improve the analyses and estimation procedures. This resulted in changes to the number of trip types, the district boundaries, and effort estimation procedures. In 2008, the CRFS program will begin to conduct studies to verify the estimates of effort for night fishing and for boats that depart from and return to private marinas. For more information: http://www.dfg.ca.gov/marine/crfs.asp

State Finfish Management Project

In 2007, a comprehensive description of the California Halibut Trawl Grounds (CHTG) fishery was prepared for the Commission. Commencing 1 April 2008, approximately 73 square nautical miles within the CHTG located in state waters off of Ventura and Santa Barbara Counties are proposed to be closed (Fish and Game Code [FGC] §8495). The Fish and Game Commission has the authority to reverse the pending closures if fishery performance criteria listed in FGC §8495 for this fishery are met. Sampling began in the commercial California halibut fishery in central California for basic

length, weight, sex, and age-composition data. Sublegal halibut were tagged and released. These data along with similar data from previous efforts in southern California will be used in a planned stock assessment for California halibut (*Paralichthys californicus*).

In 2007, a recreational beach fishery study began in central and southern California counties examining the barred surfperch (*Amphistichus argenteus*). The program uses a series of "progressive angler surveys," recording instantaneous angler counts at major beach fishing locations on random days. Recommendations will be made to the CFRS sampling program regarding beach and bank fishing modes to improve total catch and effort estimates.

In 2007, the California commercial hagfish fishery (primarily *Eptatretus stoutii*) experienced a resurgence in directed catch after a 17-year hiatus; landing in excess of 1 million lbs for the first time since 1990. In response the Project is tracking fishery landings statewide, and sampling the fishery for size composition since this is one of the last open access fisheries in the state.

Marine Project Reviews

Marine Project Review staff reviewed and evaluated proposed projects that have the potential to affect marine resources, habitats, and water quality, especially as they relate to threatened and endangered species and essential fish habitats. During 2007–08, some of these projects included liquefied natural gas projects, oil platform decommissioning projects, state and federal marine aquaculture programs, the Federal Energy Regulatory Commission's Wave Energy permitting process, as well as desalination projects in both northern and southern California.

Fishery-Independent SCUBA Assessment Project

In 2007, CDFG created a new Fishery-Independent SCUBA Assessment Project. Using SCUBA-based methods, the staff of this project conducts surveys of fish and invertebrates in nearshore subtidal habitats, inside and outside Marine Park Areas (MPAs). This project, in partnership with other agencies and academic institutions, is a collaborative research and monitoring program. In southern California, the project is collecting data on surfperch and other nearshore sandy beach fishes through beach seining and mark-recapture efforts. Data are being collected on the movement patterns of barred sand bass (*Paralabrax nebulifer*), particularly in relation to their spawning behavior. In central California, the abundance, mortality, and movement patterns of rocky reef fishes listed in CDFG's Nearshore Fishery Management Plan is being investigated. In addition, data are being collected to estimate age, growth, and maturity of kelp greenling.

ROV and Kelp Surveys

CDFG, along with the Pacific States Marine Fisheries Commission and its partners, have been using a Remotely Operated Vehicle (ROV) to quantitatively survey deep subtidal habitats. The Department has been conducting ROV surveys within and adjacent to the Channel Islands Marine Protected Areas since 2003. This effort was expanded in 2007 when the Department conducted the first annual surveys in the Central Coast Marine Protected Areas from Monterey Peninsula to Point Lobos. Recent work is focused on developing the ability to measure fishes using paired lasers.

During 2007 the CDFG completed the sixth annual coast-wide survey of California's kelp beds. The results of ongoing aerial assessments through 2006 are now available to GIS users on the Department's website at: http://ftp.dfg.ca.gov/Public/R7_MR/Natural_Resources/Kelp/

Marine Life Protection Act

The Marine Life Protection Act is being implemented in five planning regions which encompass the California coastline and is expected to be completed by 2011. The first planning region, along the central coast from Pigeon Point in San Mateo County south to Point Conception in Santa Barbara County, was completed in April 2007, when the California Fish and Game Commission adopted 29 MPAs. These 29 MPAs represent approximately 204 square miles (or approximately 18 percent) of state waters, with 85 square miles designated as no-take state marine reserves, and became effective in September 2007. The second planning region process commenced in summer of 2007, in the north-central coast region, from Pigeon Point to Alder Creek, near Point Arena, Mendocino County. A Blue Ribbon Task Force, appointed by the Secretary for Resources, will make its recommendation for a preferred proposal to the Fish and Game Commission in May 2008. The Commission's formal public process will commence at that time. See www.dfg.ca.gov/mlpa for more information.

Ocean Salmon Project

In April 2008, the California Fish and Game Commission voted unanimously to prohibit commercial and recreational salmon fishing in state ocean waters, which extend three miles off the coast. This followed a federal ban imposed by the Pacific Fishery Management Council which applies to U.S. waters extending from three to 200 miles off the coasts of California and Oregon. The Commission took this unprecedented action based on sharp declines in runs of fall-run Sacramento Chinook salmon.

In 2007, ocean salmon fisheries in California were less constrained than 2006 due to a forecasted increase in the ocean abundance of Klamath River fall Chinook;

however, these forecasts did not materialize as Chinook landings in the California recreational and commercial fisheries were the lowest and second lowest, respectively, on record since monitoring began in the 1960s. These low numbers were due primarily to a scarcity of Central Valley salmon stocks in California waters. In 2007, the salmon program sampled over 53,000 salmon in the ocean fisheries and processed 6,200 Coded Wire Tags from adipose fin-clipped salmon collected in the ocean and inland salmon fisheries, Department hatcheries, and Central Valley spawning ground surveys.

Ocean Protection Council

In 2007, the Ocean Protection Council, in partnership with the Marine Region of the California Department of Fish and Game, earmarked funds for projects and equipment upgrades for the next three years. A series of projects have been identified ranging from larval invertebrate and fish assessments, fish trapping, SCUBA surveys and MLPA baseline surveys, as well as socio-economic studies. A total of $6.7 million has been allocated for these projects. An additional $0.7 million is slated for data analysis including fishery landings e-tickets and commercial logbooks database upgrades. Furthermore, $0.45 million will target program support and staff training as well as infrastructure upgrades for vessels, ROV, and SCUBA equipment.

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REVIEW OF SOME CALIFORNIA FISHERIES FOR 2007: COASTAL PELAGIC FINFISH, MARKET SQUID, DUNGENESS CRAB, CALIFORNIA SPINY LOBSTER, HIGHLY MIGRATORY SPECIES, OCEAN SALMON, GROUNDFISH, CALIFORNIA HALIBUT, HAGFISH, PACIFIC HERRING, AND RECREATIONAL

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SUMMARY

In 2007, commercial fisheries landed an estimated 172,125 metric tons (t) of fishes and invertebrates from California ocean waters (fig. 1). This represents an increase of over 13% from the 152,088 t landed in 2006, and a 32% decline from the peak landings of 252,568 t in 2000. The preliminary ex-vessel economic value of commercial landings in 2007 was nearly $120 million, a decrease of 8% from the $130 million in 2006.

Pacific sardine was by far the largest volume fishery in the state at nearly 81,000 t, but third in ex-vessel value at $8.2 million. Market squid was second in landings at over 49,000 t, and was the highest valued fishery in the state at $29.1 million. The other top-five volume fisheries included northern anchovy at 10,400 t, red sea urchin at 5,050 t, and Pacific mackerel at 5,018 t. The ex-vessel value of Dungeness crab dropped to second in 2007 at $26.8 million, a decline of 85% from the record annual harvest in 2006. The other top-five valued fisheries include Pacific Chinook salmon at nearly $7.8 million, California spiny lobster at nearly $6.9 million, and red sea urchin at $5.0 million.

Dungeness crab landings for 2007 dropped to less than 5,000 t, a 58% decline from the record landings for 2006. Historically, the fishery peaks in a ten-year cycle. Commercial landings for California spiny lobster also declined to 300 t, a 26% decline from 2006. Starting in 2008, recreational lobster fishermen will need to carry and complete a Spiny Lobster Report Card which will be used to track recreational catch and effort.

For highly migratory species, commercial and recreational landings of albacore in California increased over 300%, although landings along the entire West Coast were down in 2007. Landings of all other tuna species increased slightly with the exception of skipjack. Landings of swordfish increased 46% over 2006. In 2007, the California Fish and Game Commission (Commission) adopted bag limits for both albacore and bluefin tuna consistent with federal regulations.

In 2007, California ocean salmon fisheries were less constrained than in 2006 due to a higher forecasted abundance of Klamath River Fall Chinook (KRFC). Commercial fisheries had 141 more days open than in 2006. Estimated total commercial landings were 113,400 Chinook (686 t), which was the second lowest catch on record; however, this was still a 45% increase in weight compared to 2006 (lowest catch on record). Recreational fisheries had 90 more days open than in 2006. Estimated total recreational landings were 47,600 Chinook. This is the lowest catch on record and a 51% decrease compared to 2006. Estimated effort was 105,700 angler days, a 16% decrease from 2006. The catch per unit effort was 0.5 fish per angler, a 41% decrease from 2006.

California's commercial groundfish harvest for 2007 was over 10,000 t, a 13% decrease over 2006 landings. Pacific whiting, Dover sole, and sablefish continued to be the top species landed. The ex-vessel value of groundfish landings for 2007 was $15.9 million, 8% higher than in 2006. The first stock assessment for blue rockfish was completed in 2007.

For California halibut, new regulations have closed portions of the traditional halibut trawl grounds and implemented a restricted access program which has resulted in a decrease in landings from a peak of 596 t in 1999 to a low of 174 t in 2007. Pacific hagfish landings in California increased ten-fold from 77 t in 2006 to 773 t in 2007, the result of increased demand in South Korean markets for human consumption. Pacific herring landings in California dropped to the second lowest level in the 35-year history of the fishery, thought to be the result of a decrease in length at age of the fish and increased competition from other herring fisheries world-wide.

Over 541,000 recreational anglers caught nearly 2.7 million fish and invertebrates aboard Commercial Passenger Fishing Vessels (CPFVs) in California in 2007, a 10% decline from the 3.0 million landed in 2006. Rockfishes (all species combined), kelp bass, and California scorpionfish, barred sandbass, and California barracuda were the top species landed.

In 2007, the Commission undertook 14 rule-making actions that address marine and anadromous species. The Commission adopted changes to albacore, bluefin tuna, salmon, groundfish, sea urchin, abalone, herring, and rock crab regulations and added the recreational Spiny Lobster Report Card. The Commission also established 15 marine protected areas (528 square kilometers, 204 square

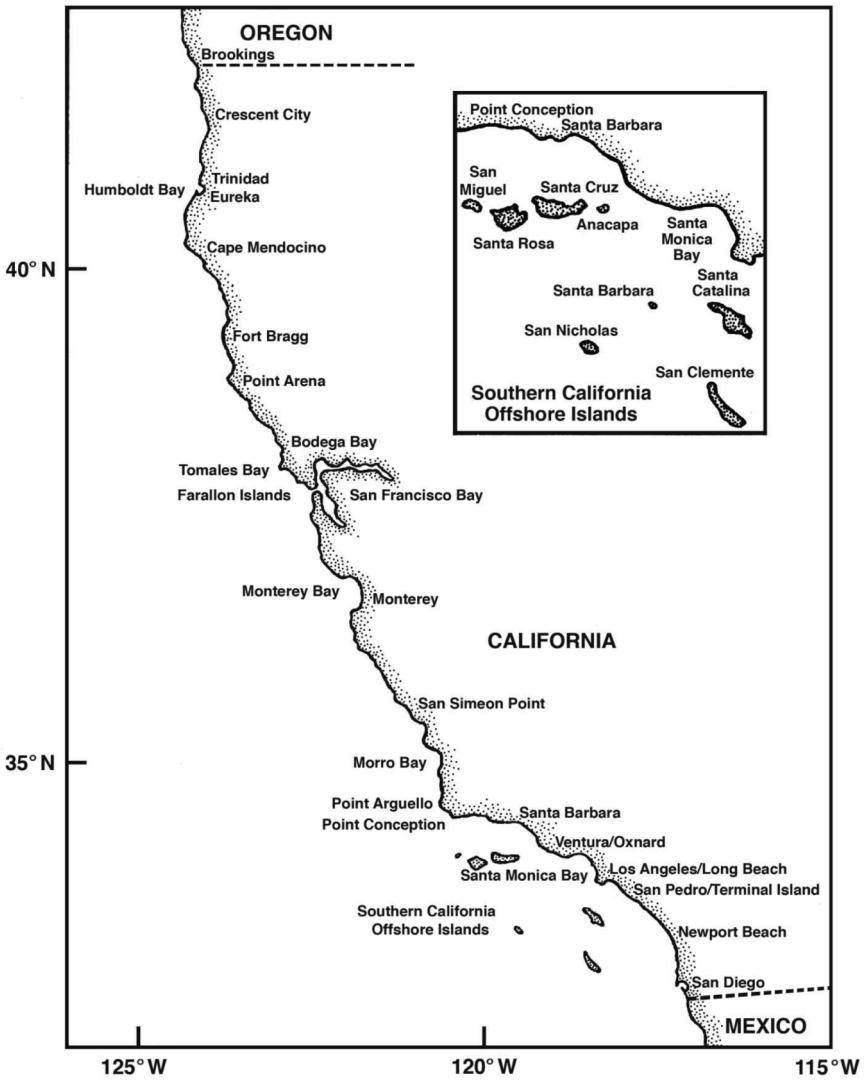

Figure 1. California ports and fishing areas.

miles) in central California from Pigeon Point in San Mateo County south to Point Conception in Santa Barbara County, and approved the establishment of federal marine protected areas adjacent to the previously established Channel Islands marine protected areas under the Marine Life Protection Act. In addition, the Commission was petitioned to increase protections for two anadromous Osmerids: to uplist the delta smelt from threatened to endangered and to list the longfin smelt as endangered.

Coastal Pelagic Finfish

Pacific sardine (*Sardinops sagax*), Pacific mackerel (*Scomber japonicus*), jack mackerel (*Trachurus symmetricus*), and northern anchovy (*Engraulis mordax*) form a finfish complex known as coastal pelagic species (CPS). These species are jointly managed by the Pacific Fishery Management Council (PFMC) and NOAA's National Marine Fisheries Service (NMFS). In 2007, total commercial landings for these species equaled 96,990 t (tab. 1), and was valued at nearly $10.3 million in ex-vessel revenue. Compared to landings in 2006, this represents a 46% and 40% increase in quantity and ex-vessel value, respectively. Once again, Pacific sardine ranked as the largest fishery among these four species, contributing 83% of the combined quantity and 80% of the combined ex-vessel value.

Pacific Sardine. In 2007, the total quantity of Pacific sardine landed (80,950 t) was 73% greater than in 2006 (46,762 t). This is the largest amount of Pacific sardine landed in California since the late 1960s and generated an ex-vessel value of more than $8 million. Commercial landings of sardine averaged 50,236 t over the ten-year period from 1998–2007 (fig. 2). Nearly all (96%) of California's 2007 sardine catch was landed in Los Angeles

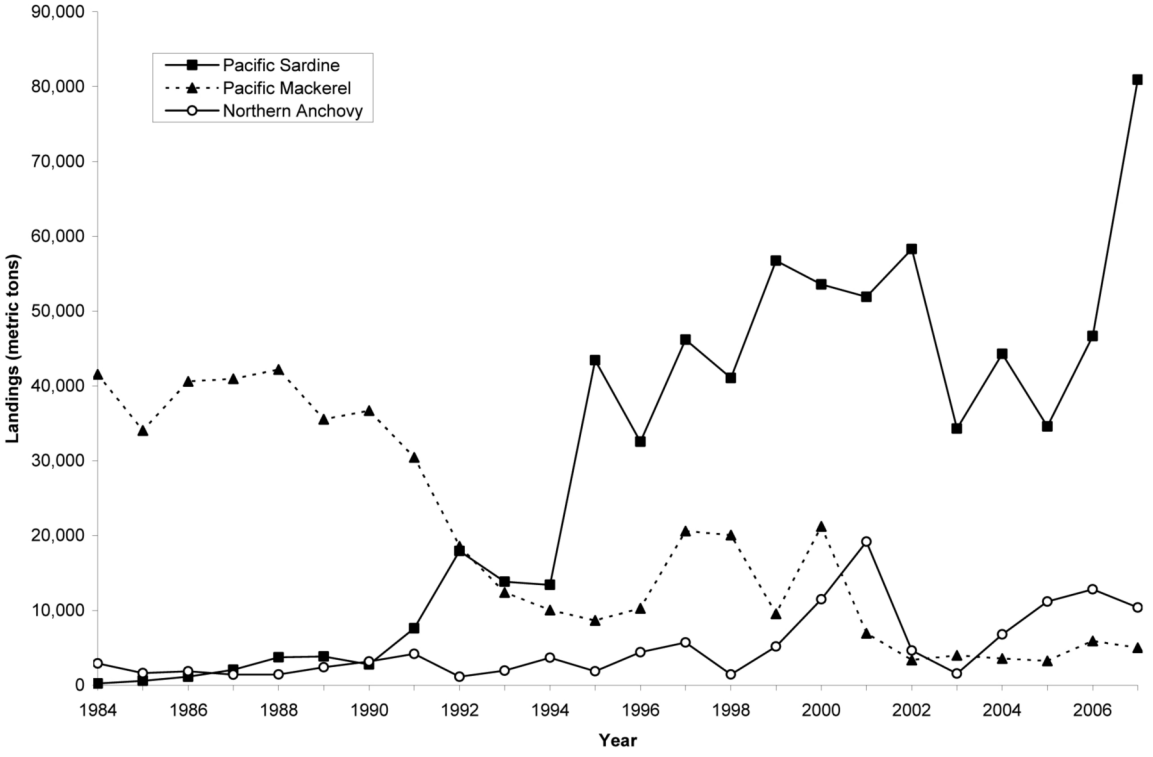

Figure 2. California commercial landings of Pacific sardine (*Sardinops sagax*), Pacific mackerel (*Scomber japonicus*), and northern anchovy (*Engraulis mordax*) 1984–2007.

TABLE 1
Landings of Coastal Pelagic Species in California (metric tons).

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
1977	5	99,504	5,333	44,775	5,200	12,811	167,628
1978	4	11,253	11,193	30,755	4,401	17,145	74,751
1979	16	48,094	27,198	16,335	4,189	19,690	115,542
1980	34	42,255	29,139	20,019	7,932	15,385	114,764
1981	28	51,466	38,304	13,990	5,865	23,510	133,163
1982	129	41,385	27,916	25,984	10,106	16,308	121,828
1983	346	4,231	32,028	18,095	7,881	1,824	64,405
1984	231	2,908	41,534	10,504	3,786	564	59,527
1985	583	1,600	34,053	9,210	7,856	10,275	63,577
1986	1,145	1,879	40,616	10,898	7,502	21,278	83,318
1987	2,061	1,424	40,961	11,653	8,264	19,984	84,347
1988	3,724	1,444	42,200	10,157	8,677	36,641	102,843
1989	3,845	2,410	35,548	19,477	9,046	40,893	111,219
1990	2,770	3,156	36,716	4,874	7,978	28,447	83,941
1991	7,625	4,184	30,459	1,667	7,345	37,388	88,668
1992	17,946	1,124	18,570	5,878	6,318	13,110	62,946
1993	13,843	1,954	12,391	1,614	3,882	42,708	76,392
1994	13,420	3,680	10,040	2,153	2,668	55,395	85,929
1995	43,450	1,881	8,667	2,640	4,475	70,278	131,391
1996	32,553	4,419	10,286	1,985	5,518	80,360	135,121
1997	46,196	5,718	20,615	1,161	11,541	70,257	155,488
1998	41,056	1,457	20,073	970	2,432	2,709	68,646
1999	56,747	5,179	9,527	963	2,207	90,322	164,945
2000	53,586	11,504	21,222	1,135	3,736	117,961	209,144
2001	51,811	19,187	6,924	3,615	2,715	85,828	170,080
2002	58,353	4,643	3,367	1,006	3,339	72,878	143,586
2003	34,292	1,547	3,999	155	1,780	44,965	88,741
2004	44,293	6,793	3,569	1,027	1,596	40,324	99,606
2005	34,599	11,178	3,243	199	219	55,407	104,845
2006	46,672	12,815	5,904	1,169	37	49,248	115,845
2007	80,950	10,390	5,018	632	597	49,438	147,025

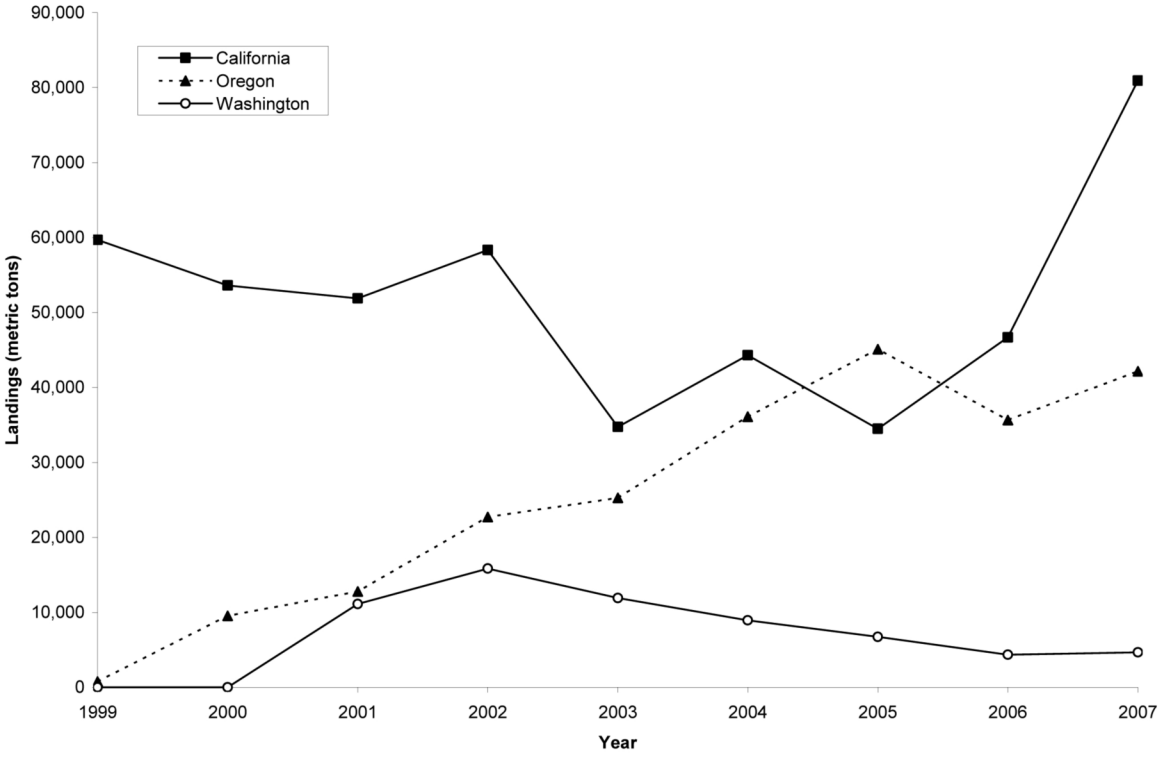

Figure 3. Commercial landings of Pacific sardine (*Sardinops sagax*) in California, Oregon, and Washington, 1999–2007.

TABLE 2
Landings (metric tons) of Pacific sardine (*Sardinops sagax*) and Pacific mackerel (*Scomber japonicus*) at California port areas in 2007.

	Pacific sardine		Pacific mackerel	
Area	Landings	% Total	Landings	% Total
Eureka	0	0	0	0
San Francisco	2	0	0	0
Monterey	34,756	43	123	2
Santa Barbara	3,208	4	9	0
Los Angeles	42,984	53	4,885	97
San Diego	0	0	0	0
Total	80,950	100	5,018	100

(53%, 42,966.2 t) and Monterey (43%, 34,755.8 t) port areas (tab. 2).

In keeping with the increased California landings for 2007, California exports of sardine increased by 43% over 2006 exports (46,762 t). A total of 66,896 t of sardine product was exported to 37 countries. The majority (83%) of this product was exported to Thailand (20,463 t), Australia (18,498 t), Brazil (9,632 t), and Japan (7,061 t). These four countries represent 80% of the total export value of nearly $40.4 million.

The Pacific sardine fishery ranges from British Columbia, Canada, southward to Baja California, Mexico. The majority of landings occur in southern California and northern Baja California. However, since the expansion of the sardine fishery in 1999, landings have steadily increased in the Pacific Northwest. The combined landings of Pacific sardine for California, Oregon, and Washington totaled 127,597 t, up 47% from the 86,682 t landed in 2006. The Pacific sardine harvest guideline (HG) for each calendar year is determined from the previous year's stock biomass estimate (≥1-year-old fish on 1 July) in U.S. and Mexican waters. The recommended HG for the 2007 season was 152,564 t based on a biomass estimate of 1.3 million t. This was 28% higher than the HG for 2006. The Pacific sardine HG was apportioned coast-wide through the year with 35% allocated from 1 January through 30 June, 40% plus any portion not harvested allocated from 1 July through 15 September, and the last 25%, plus any portion not harvested from the first two allocations, released on 15 September. The U.S. West Coast fisheries harvested a greater proportion (84%) of the HG compared to 2006 (69%). PFMC and NMFS will formally review this allocation scheme in 2009.

The steady increase of sardines landed in Oregon since 1999 may have leveled off or slowed in the last three years (fig. 3). Oregon landings of sardine totaled 42,144 t in 2007, a slight increase over 2006 (35,648 t). In 2007, they exported 12,483 t of sardine product worth over

$8.4 million. Brazil and Thailand received 70% of the exported sardines.

Washington landings of Pacific sardine have decreased to 4,665 t in 2007 since a peak in 2000 (15,832 t) (fig. 3). This is only slightly higher than 2006 (4,362 t). Washington exported more sardine than they landed (30,118 t), possibly product that was landed in Oregon or California.

The 2008 proposed HG is 89,093 t or 42% less than the HG for 2007. Because of the potential of the fishing industry to meet or exceed the HG, a 10% set aside for an incidental fishery was adopted. Should landings in the directed fishery exceed the allocation, Pacific sardines will be limited to 20% by weight when landing mixed loads of CPS. Should the incidental set aside for that allocation also be exceeded, the sardine fishery will be closed until the next allocation is released.

Pacific Mackerel. Pacific mackerel landings in California continue to be relatively low, with 5,018 t in 2007 (tab. 1) following a six-year trend (fig. 2). The vast majority of this catch was landed in Los Angeles port areas (tab. 2). The total ex-vessel value generated for Pacific mackerel in 2007 was $782,370. Industry exported 2,157 t of mackerel product, valued at nearly $2.1 million, to 18 countries. Indonesia (397 t), Philippines (298 t), China (291), and Egypt (242 t) received over half (57%) of this product.

Oregon reported 702 t of Pacific mackerel landed in 2007 for a total ex-vessel value of $82,608. This is up slightly from the 2006 catch of 665 t. No landings of mackerel have been reported in Washington since 2005. Washington landings of Pacific mackerel are typically low, with an annual average of 80 t (unspecified mackerel) since 1999.

Similar to sardines, the majority of Pacific mackerel landings occur in southern California and Ensenada, BCM. In the U.S., the fishing season for Pacific mackerel is 1 July to 30 June the following year. At the start of the 2007–08 season, NMFS estimated the biomass at 359,290 t, and PMFC set the HG at 40,000 t. These values are higher than the prior season (biomass: 112,700 t; HG: 19,845 t) due to changes in the modeling parameters used for stock assessment. Landings above the HG would be constrained by an incidental catch rate of 45% by weight when landed with other CPS.

Jack Mackerel. In 2007, jack mackerel landings represented less than 1% of the total catch of CPS in California with 632 t landed. This is nearly half of the total 2006 catch (1,169 t) and generated $144,167 in ex-vessel value. Landings in Oregon continue to be low with 14 t landed in 2007 for an ex-vessel value of $1,493. Washington reported no landings of jack mackerel during 2007.

Northern Anchovy. Landings of northern anchovy in California have been reported since 1916. Historically, anchovy was reduced to oil or fish meal and the fishery was modest compared to Pacific sardine and Pacific mackerel. However, periods of low sardine abundance saw increased anchovy landings. Peak landings were seen in the early- to mid-1970s with total annual harvest exceeding 100,000 t at times. Today, landings of northern anchovy are relatively modest, averaging about 8,500 t per year over the last 10 years (fig. 3). The vast majority of northern anchovy are landed in California, with occasional landings in Oregon and Washington. Anchovy are currently used for human consumption, animal food and live bait,.

Three stocks of northern anchovy are identified: northern, central, and southern. California fishery harvests are taken from the central stock which ranges from northern Baja California, Mexico, to San Francisco, California. Studies of scale deposits on the sea floor suggest that anchovy abundance can be quite high at times. At this time, the CPS fishery management plan (FMP) regards northern anchovy as a monitored species, with no requirements for formal annual assessments.

California landings of northern anchovy in 2007 amounted to 10,390 t with an ex-vessel value of nearly $1.2 million (tab. 1). This is 81% of total 2006 landings (12,815 t), but anchovy still ranked as the second most valuable CPS finfish after Pacific sardine. Exports of northern anchovy product from California totaled 357 t for an export value of $339,717. Of the eight countries that received anchovy product from California, Australia received the majority (81%).

For 2007, there were no reported landings of northern anchovy in Oregon. Washington reported 153 t valued at $35,883 ex-vessel value for 2007. Less than one metric ton was exported to Canada.

Pacific Bonito. From 1999–2007, annual Pacific bonito (*Sarda chiliensis lineolata*) landings averaged 439 t, a small percentage of the total CPS quantity landed in California. In 2007, landings dropped 91% from last year's high of 2,491 t to 222 t. The landings generated an ex-vessel value of $158,853. No landings of Pacific bonito were reported from Oregon or Washington in 2007.

California Market Squid

In 2007, market squid (*Loligo opalescens*) was California's largest fishery for ex-vessel value and second to Pacific sardine in quantity. Total landings in the squid fishery were 1% more than in 2006, increasing from 49,150 t to 49,801 t (fig. 4). The ex-vessel price ranged from $22–$1,654/t, with an average of 597/t (an increase compared to the 2006 average of $560/t). The 2007 ex-vessel value was approximately $29.3 million, a 9% increase from 2006 ($26.9 million). Market squid remains an important international commodity and is used domesti-

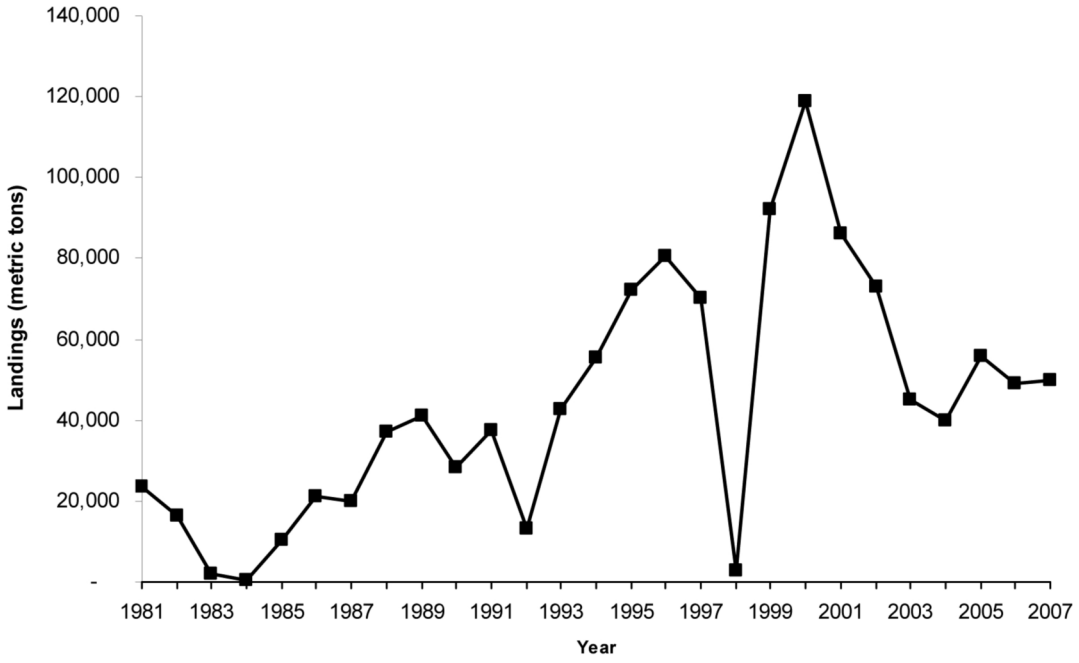

Figure 4. California commercial market squid (*Loligo opalescens*) landings, 1981–2007.

cally for food and as bait by the recreational fishery. Approximately 25,025 t of market squid were exported for a value of $32.9 million in 2007. Asian countries were the main export market with about 82% of the trade going to China (16,910 t) and Japan (3,489 t). Approximately 9% of the trade went to England (770 t), Spain (690 t), and Australia (590 t). The remaining 9% was exported to 37 other countries. Unlike last year, no market squid was exported to Switzerland. In 2006, Switzerland accounted for 19% of the total export trade and was the second only to China.

The market squid fishery uses either seine or brail gear that is usually combined with attracting lights to capture spawning adult squid aggregations swimming in shallow water. While most fishing effort occurs at night, spawning in some areas has been observed during the day. Spawning may occur year-round; however, generally the fishery is most active from April to September in northern regions (north of Point Conception) of California and from October to March in southern regions (south of Point Conception).

The fishing permit season for market squid extends from 1 April through 31 March of the following year. During the 2007–08 season (as opposed to the 2007 calendar year) 45,813 t were landed, a 32% increase from the 2006–07 season (34,809 t). There was a 90% decline in catch from the northern fishery near Monterey in the 2007–08 season with only 53 t landed (fig. 5), and was likely influenced by the La Niña/Southern Oscillation event. Low landing numbers in this region often coincide with La Niña events. However, this landing total is exceptional because it is the lowest since the 1998–99 landings (24 t). The 1998–99 season, which also occurred during a La Niña, was a hallmark season because it had the lowest landing total in the northern region since monitoring of squid began in the 1930s. Although the northern region harvests steadily climbed after the 1998–99 season to peak at 25,242 t in the 2002–03 season, the low harvests for the northern region during the 2007–08 season is a concern for management.

In contrast, landings of market squid in California were almost exclusively taken from the southern California region during the 2007–08 season, accounting for 99.9% of the total catch with 45,759 t landed (fig. 5). This regional domination of catch last occurred during the 1998–99 and 1999–00 seasons (99.7% and 99.8% respectively) and may be influenced by coinciding La Niña events. At the start of the 2007–08 season, squid fishing was centered off northern Channel Island coastlines of Santa Cruz and Santa Rosa. However, at the end of the season, fishing was centered on the west coast of Santa Catalina Island and along the coastline of La Jolla. This varies from the 2006–07 season where major landings were absent from Santa Catalina and La Jolla.

Dungeness Crab

Landings of Dungeness crab (*Cancer magister*) totaled 4,969 t in 2007, a 58% decrease from the 11,867 t landed in 2006. The 2006 catch total is an artifact of the statutory postponement of the northern California 2005–06

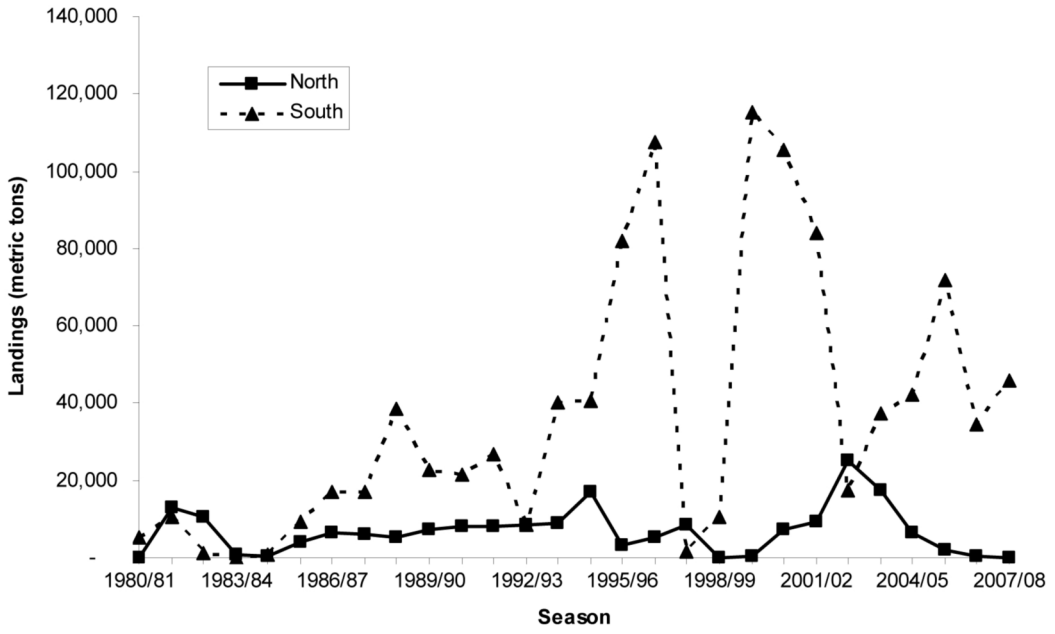

Figure 5. Comparison of market squid landings for northern and southern fisheries by fishing season (1 April–31 March), from 1980–1981 to 2007–2008 seasons.

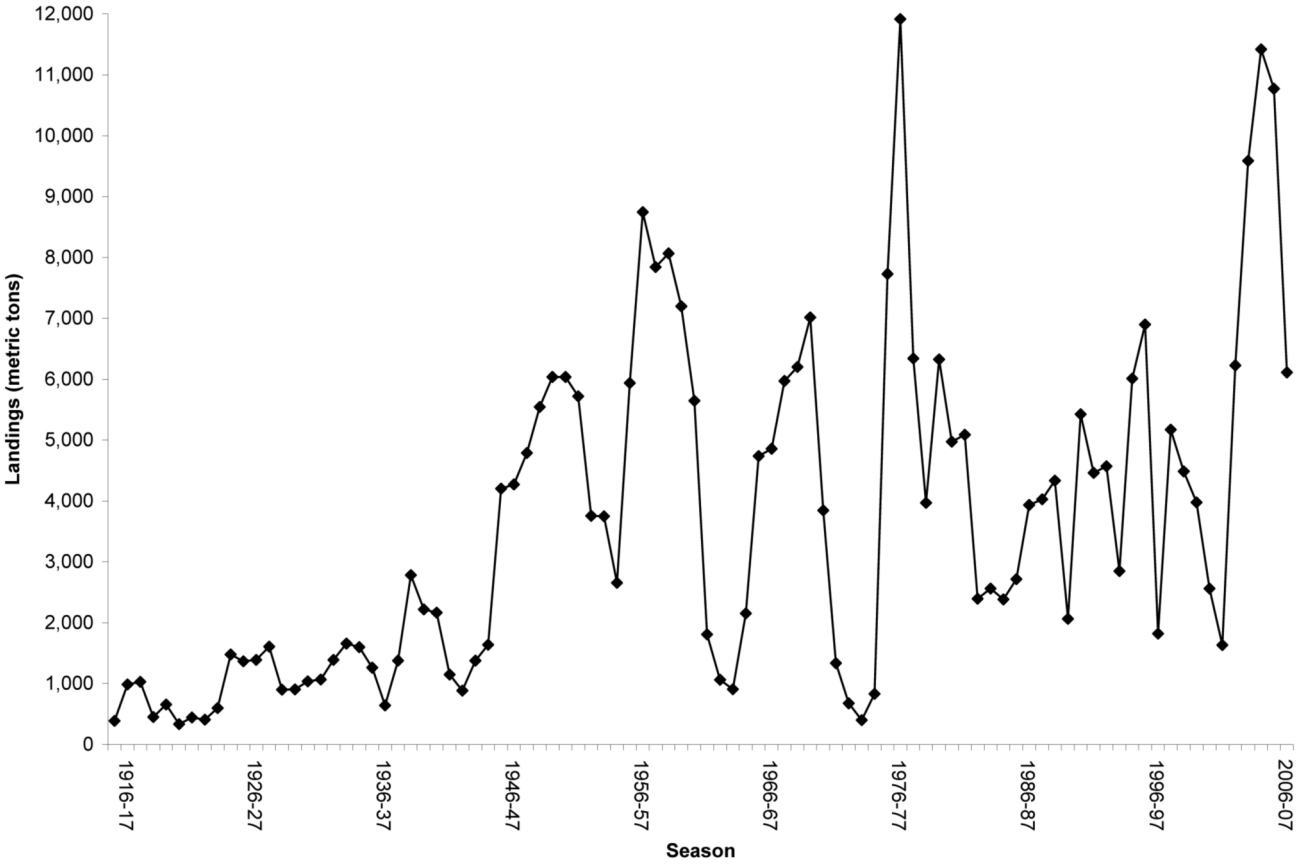

Figure 6. California commercial Dungeness crab (*Cancer magister*) landings by season (15 November–15 July), 1916–1917 to 2006–2007.

season opening, due to poor crab condition. The 2005–06 northern California season opener was delayed by the California Department of Fish and Game (CDFG), for the first time since given that authority in 1995, until the last day of 2005 to allow ample time for crab condition to improve.

The commercial Dungeness crab fishery is managed using a combination of technical measures: size, sex, and season restrictions. Only male crabs with a carapace width larger than 159 mm (6.25 in) are harvested commercially. The minimum size limit is designed to protect sexually mature male crabs from harvest for at least one season. This provision appears to be successful because northern California studies have shown, despite the presumption that nearly all legal-sized male crabs are harvested each season, that almost all sexually mature female crabs are fertilized each year. The central California season, south of the Mendocino/Sonoma county line, begins 15 November and ends 30 June. The northern California season conditionally begins on 1 December and ends 15 July. The timing of the seasons avoids the portion of the life-cycle when most crabs are molting or soft-shelled.

Commercial landings of Dungeness crab for the 2006–07 season totaled 6,109 t, just under the10-year running average of 6,194 t per fishing season (fig. 6). The catch was a 43% decrease from the 10,769 t landed in the 2005–06 season, the third highest season on record. Historically, the fishery has been cyclical, with abundance peaking approximately every ten years. Despite the large decline in catch, ex-vessel value remained high for 2006–07 at $30.4 million. This was only a 23% decrease from the previous season, which was the most valuable season on record. The average price paid to fishermen was $5.69/kg ($2.58/lb) and a good spring catch and high prices from March to July helped increase the season's value.

The fishery is also managed by limited entry. There were 519 resident vessel permits and 89 non-resident permits renewed in 2007 for a total of 608 permits. Of those, 418 boats made at least one landing in the 2006–07 season. There is no limit to the number of traps a permitted boat may fish or the frequency with which they are fished. As the groundfish industry has declined, larger multi-purpose vessels have devoted more effort to Dungeness crab. According to a 2003 CalCOFI report based on a fisherman survey, there were at least 172,000 traps being fished in California during the 2001–02 season. In 2006, fishermen roughly estimated 150,000 traps being fished, but no official estimates are available. In Oregon's Dungeness crab fishery the estimated number of traps soared from 150,000 in 2002 to 200,000 in 2005 before implementation of a trap limit. Complaints of overcrowded fishing grounds, in central California in particular, have increased in recent years.

For Californian crab fishermen, recent fishery issues have centered on the apparent increasing amount of effort in terms of traps deployed in both central and northern California. However, the Dungeness crab fishery has always had a derby aspect where much of the total catch is caught in a relatively short period of time at the beginning of the season. For example, in the 2006–07 season, 79% of the total catch was landed by 1 February—only two months after the northern season opened.

California Spiny Lobster

Commercial landings in 2007 for California spiny lobster (*Panulirus interruptus*) totaled 300 t, the lowest landings for a calendar year since 1999 (fig. 7). Increases and decreases in landings are not unexpected considering that this fishery is strongly influenced by the weather and El Niño/Southern Oscillation (ENSO) events. In 2007, landings were split between ports in San Diego County (32%), Los Angeles/Orange counties (35%), and Santa Barbara/Ventura Counties (33%). Landings in previous seasons had been highest in San Diego, followed by Santa Barbara/Ventura, and then Los Angeles/Orange Counties. The ex-vessel value of the lobster fishery was $7.32 million in 2007, down from $8.06 million in 2006. California ex-vessel prices for spiny lobster consistently range from $15.43 to $26.46/kg. The spiny lobster catch is primarily exported to Asian markets, so prices depend on the strength of these overseas markets as well as the foreign currency exchange rates. In recent years, there has been an effort to develop a domestic market. However, results have been limited, partly due to the availability of American lobsters (*Homarus americanus*) at a lower cost.

A commercial fishery for California spiny lobster has been present in southern California waters since the late 1800s, and landings have been recorded by the CDFG since 1916 (fig. 7). Fishermen use baited traps that are individually set and buoyed to capture lobster alive. There is also a recreational fishery which allows lobsters to be caught by hand, using snorkeling gear, scuba diving, or by using baited hoop nets. Up to five baited hoop nets per person, with a maximum of ten hoop nets per boat can be used. Anecdotal evidence suggests that this method of take is growing in popularity. In recent years, a modified hoop net with a rigid structure has been introduced to the recreational fishery. Recent CDFG studies suggest that this new type of hoop net is much more effective at catching lobster than the traditional style hoop net. Commercial and recreational fishermen take lobster in shallow, rocky areas from Point Conception south to the U.S.-Mexico Border and at offshore banks and islands. Lobster season for both recreational and commercial fishermen runs from late September or early

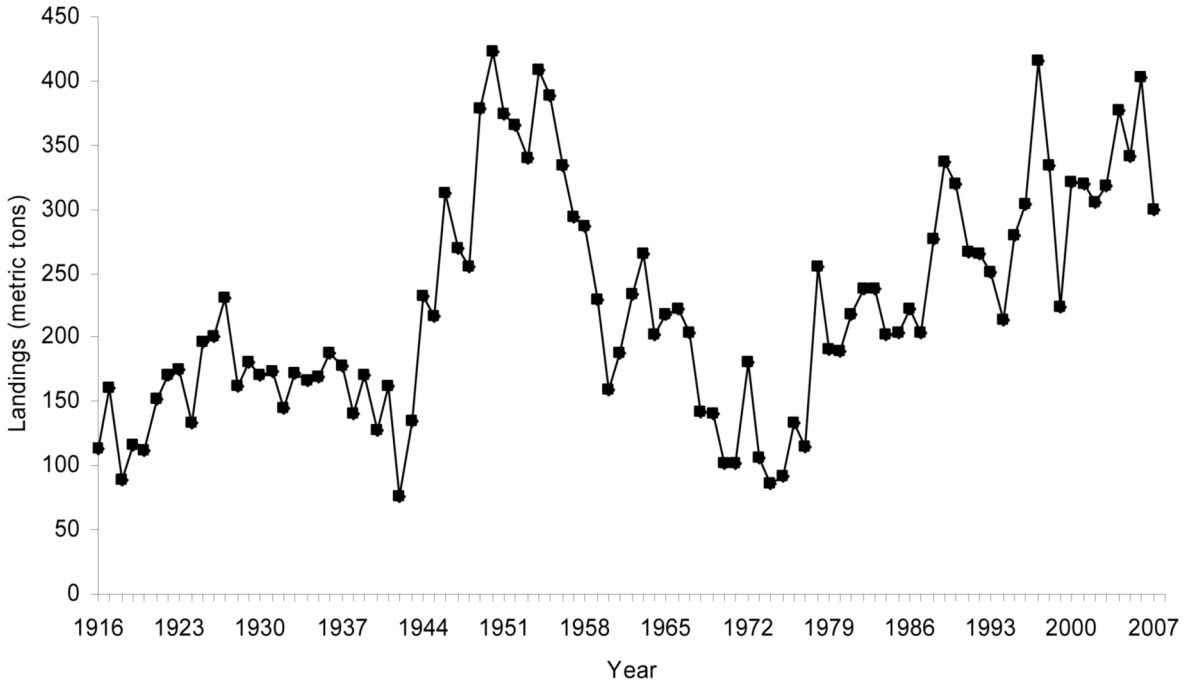

Figure 7. California landings of California spiny lobster (*Panulirus interruptus*) from 1916 to 2007.

October through mid-March to protect the spawning season, and the majority of the landings occur in the first few months of the season.

Since the 1950s, there have been several major regulation changes aimed at better managing the lobster fishery. In 1955, a minimum-size limit of 8.26 cm (3.25 in.) carapace length was established for both recreational and commercial fishermen. Since the 1976–77 season, commercial fishermen have been required to use rectangular escape ports (6.05 cm x 29.2 cm) (2.38 in. x 11.5 in.) on traps to decrease the retention of undersized lobster.

A restricted access program for the commercial take of spiny lobster was initiated in the 1996–97 season after a two-year moratorium on permits. Although the number of active participants varies little from season to season, the number of lobster operator permits declines every year. In the 2006–07 season, a total of 214 permits were renewed, with only 153 actively fishing lobster. Prior to 2003, a small number (three or less) of new permits were issued via a lottery to qualified lobster crewmembers. In February 2003, the Commission repealed the permit lottery and the capacity goal of 225 fishermen. This was done in anticipation of a formal review of the fishery to be conducted by CDFG, which did not take place as planned. Consequently, the industry returned to the Commission in 2004 and requested that an industry regulatory proposal allowing transferability of qualifying lobster permits be considered. The CDFG and the industry worked together to craft a transferability program that would not result in a large increase in trap effort. The Commission approved the proposal and a percentage of the existing permits became transferable. For the first three fishing seasons thereafter (2005–06 through 2007–08), transfers were limited to the first ten permittees that applied. Since 1 April 2008, there are no restrictions on the number of permits that can be transferred.

A logbook for the commercial fishery has been required since 1973. Logbook compliance has remained high at 90% or greater, and CDFG has confidence in these effort estimates. The total number of trap pulls in the 2006–07 lobster season was estimated at 844,000. This number is less than the over 900,000 estimated trap pulls in the 2003–04 lobster season when the last review was conducted. However, the number of trap pulls has generally increased since the 1981–82 season when about 500,000 traps were pulled.

Currently, there are no limits on the amount of lobster commercial fishermen can land nor on the number of traps they can use. Fishermen set their traps along depth contours in shallow water at the beginning of the season and move them farther from shore (>30.5 m) as the lobsters migrate offshore. This offshore-nearshore migration of lobsters is stimulated primarily by water temperature. Typically, fishermen set between 100 and 300 traps, but those with larger boats or a crewmember may set more. The commercial lobster industry was

concerned about how the MPAs established in the northern Channel Islands in 2002 would affect their fishery. Recent CDFG landings data have not shown a notable decline in the lobster catch since the MPAs were established.

The new system of reporting (Spiny Lobster Report Card) beginning in the 2008–09 season, along with data collected from a CDFG lobster creel survey from the 2007–08 season, will allow CDFG's biologists to find out how many people are fishing for lobster, how long it takes to catch them, how many are being harvested, what type of gear is being used, and where the animals are being caught. With this information, biologists can estimate the total recreational catch and effort, and evaluate the health of the lobster resource and whether current management measures are effective.

Highly Migratory Species

Albacore. Albacore (*Thunnus alalunga*) is the most abundant tuna caught in both commercial and recreational fisheries in California and along the West Coast. In the commercial fishery, albacore are caught primarily using hook-and-line gear (jig/bait/troll), but they can also be caught using drift gill net or a purse seine. Along the entire West Coast 11,570 t were commercially landed in 2007. This is a decrease of almost 10% coast-wide, but in California there was an increase from 207 t in 2006 to 856 t in 2007. During this time period the ex-vessel value in California was $1.6 million and price-per-kilogram decreased slightly to $1.88/kg ($0.85/lb), bringing it equal to the coast-wide average. Most of this catch was exported for processing and canning, but a small percentage was sold for the restaurant trade.

Historically, there have been no bag or size limits on sport-caught albacore in California. In late 2006, the PFMC adopted bag limit conservation measures for albacore (10 fish south of Point Conception, 25 fish north of Point Conception). Comparable state regulations were adopted by the Commission in 2007. Most of the recreational take of albacore comes from sportfishing in Mexican waters, which has a five-fish daily bag limit. In 2007, 100,644 albacore were reported taken by California's CPFV fleet, an increase of 381% from 2006 (20,925) and 2% from 2005 (98,611).

Yellowfin Tuna. Commercial landings of yellowfin (*Thunnus albacares*) increased slightly to 104 t in 2007, but were still down from the 286 t landed in 2005. The yellowfin were landed by purse seine gear (95%), hook-and-line gear (5%), and drift gill nets (<1%). Ex-vessel value totaled $149,568 and price-per-kilogram declined to an average $1.43/kg ($0.65/lb) compared to the $4.93/kg ($2.24/lb) paid in 2006. Most of the catch was processed into canned consumer product, with some sold to the restaurant trade. Exports of fresh frozen yellowfin tuna from California went to Mexico for processing as there are currently no canneries operating in California. CPFV logbook data indicate recreational anglers landed 18,606 yellowfin, continuing the decline seen last year (approximately 45,000 in 2006 and 55,000 in 2005).

Skipjack Tuna. Commercial landings of skipjack (*Katsuwonus pelamis*) continued to decline in 2007 to 5.1 t from 48 t in 2006 and 533 t in 2005. The variable catch success is likely due to seasonal fluctuation in abundance of fish within range of southern California vessels. In 2007 the ex-vessel value decreased to an average of $0.86/kg ($0.39/lb) from $1.22/kg ($0.55/lb) average paid in 2006. Skipjack is primarily landed in California by purse seine vessels. Frozen skipjack are exported for processing into canned product. CPFV logbook data indicate that recreational anglers landed 654 fish in 2007, a decrease of 86% from 2006 (4,541).

Bluefin Tuna. Commercial landings of bluefin (*Thunnus thynnus*) increased to 44.8 t in 2007 (from 0.8 t in 2006), but this is still far less than the 207 t landed in 2005. Ex-vessel value was $58,093, and price-per-kilogram decreased to $1.30/kg ($0.59/lb) from an average $4.74/kg ($2.24/lb) in 2006. Purse seine vessels caught 95% of the bluefin landed in 2007, while in 2006 the drift gill net fleet accounted for 65% of the landings. Recreational anglers landed 1,007 bluefin in 2007, down from 7,356 fish landed in 2006. In 2007, the Commission adopted regulations in line with the PFMC conservation measure of a 10-fish bag limit for bluefin tuna.

Swordfish. Swordfish (*Xiphias gladius*) is the most valuable fish taken in the California highly migratory species (HMS) fishery. In 2007, commercial landings totaled 542 t, up 46% from the 371 t landed in 2006. The commercial catch was valued at $3.1 million. In 2007, 89% of the commercial catch came from drift gill net gear, while harpoon fishermen landed the remainder. The price-per-kilogram decreased in 2007 to an average of $5.68/kg ($2.58/lb) compared to $8.93/kg ($4.02/lb) in 2006. Swordfish caught by harpoon is considered more valuable than gill net-caught fish. Ex-vessel price-per-kilogram can exceed $11.11/kg ($5.00/lb) for harpooned fish. The recreational catch of swordfish is unknown but is considered to be very few in number.

Common Thresher Shark. Common thresher shark (*Alopias vulpinus*) is the most common shark taken in the California HMS fishery. In 2007, 95% of the commercial catch of common thresher shark came from gill net vessels. Commercial landings increased by 113% in 2007 to 198 t from 93 t in 2006. The ex-vessel value totaled $328,705, and price-per-kilogram dropped from an average of $3.16/kg ($1.42/lb) in 2006 to $1.66/kg ($0.75/lb). CPFV logbook data indicate that 54 fish were landed recreationally in 2007, double the 2006 total of

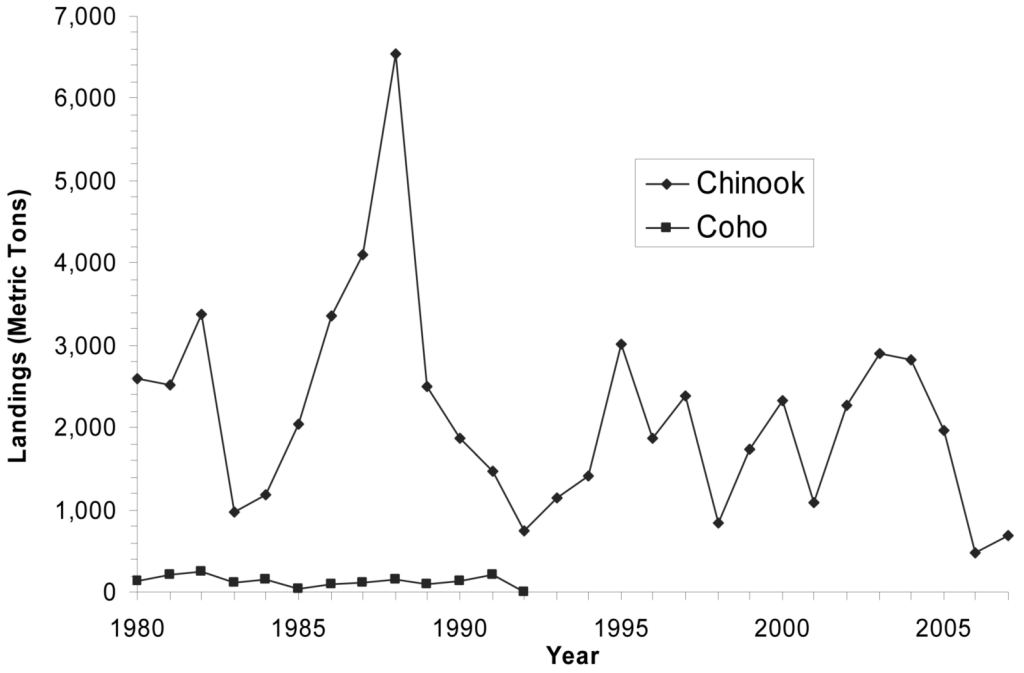

Figure 8. California commercial landings of ocean salmon from 1981 to 2007. Note: Commercial fishery landings of coho salmon (*Oncorhynchus kisutch*) were prohibited after 1992 to protect California coho salmon stocks.

27. However, recreational catches of thresher shark from private vessels may be underestimated due to the shark's increased popularity as a targeted species.

Shortfin Mako Shark. Shortfin mako shark (*Isurus oxyrinchus*) is the second most common shark landed in the commercial HMS fishery. In 2007, 74% of the commercial catch of mako shark came from drift gill net gear, 9% from set gill nets, and 13% from hook-and-line gear. Commercial landings increased 38% in 2007 to 44 t, compared to 32 t in 2006. Ex-vessel value decreased to $76,534, due to a fall in the price-per-kilogram from an average of $2.44/kg ($1.10/lb) in 2006 to $1.74/kg ($0.79/lb) in 2007. According to CPFV logbook data, 205 mako sharks were taken in 2007, a 14% decrease compared to 238 in 2006.

Dorado (dolphinfish). Commercial landings of dorado (*Coryphaena hippurus*) totaled 2.3 t in 2007, a slight decrease from the 2.9 t landed in 2006. The ex-vessel value was $10,077, and the price-per-kilogram decreased to $4.38/kg ($1.99/lb) from $6.18/kg ($2.78/lb) in 2006. Historically, dorado landings have been a relatively small component of the HMS fishery and vary from year to year, primarily depending on cyclic intrusions of warm water into the southern California waters. Local seafood restaurants purchase dorado when available. Recreational anglers landed 6,326 dorado in 2007 compared to 45,569 in 2006 and 6,654 in 2005.

2007 HMS Fishery Management Highlights. The PFMC's highly migratory species fishery management plan (HMS FMP) was approved by NMFS in March of 2004. Adoption of the HMS FMP provided for implementation of new management and conservation measures, consolidation of existing state and federal regulations, and international agreements for HMS. In 2007, the PFMC continued to focus on implementing the HMS FMP.

In 2006, the PFMC moved to amend the HMS FMP to address eastern Pacific Ocean overfishing of yellowfin tuna. This process was stalled in 2007 due to the reauthorization of the Magnuson Stevens Fisheries Conservation Act. As required by the Act, the PFMC considered the need for additional domestic regulation to address the relative impact of West Coast fisheries and recommended no additional measures. These recommendations will be reconsidered by the PFMC in 2008.

In response to resolutions adopted by the Inter-American Tropical Tuna Committee (IATTC) and Western and Central Pacific Fisheries Commission (WCPFC), the PFMC will forward to the U.S. delegations of these organizations methods to characterize fishing effort on North Pacific albacore. Based on the information provided, the PFMC concludes that U.S. West Coast effort on north Pacific albacore is not increasing.

The Commission adopted state bag limit conservation measures for the recreational harvest of albacore and bluefin tunas. These measures are in line with the PFMC measures adopted in 2006.

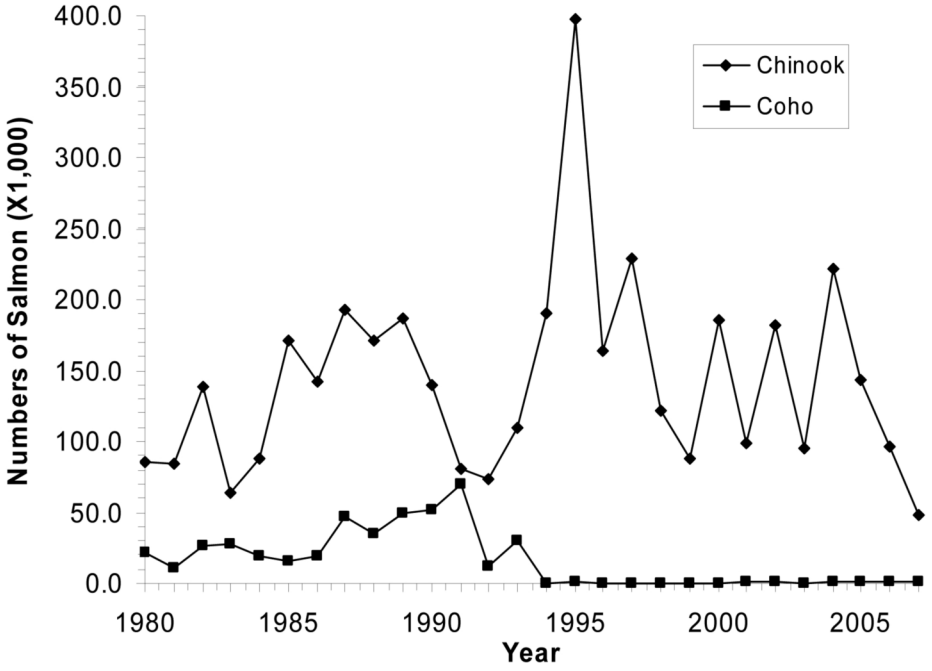

Figure 9. California recreational landings of ocean salmon from 1981 to 2007. Note: Landings of coho salmon were prohibited after 1996 to protect California coho salmon stocks. Numbers reported since 1996 are illegal harvest.

Ocean Salmon

Ocean salmon fisheries in California primarily target Chinook salmon (*Oncorhynchus tshawytscha*). The retention of coho salmon (*O. kisutch*) has been prohibited in the commercial and recreational fisheries since 1993 and 1996, respectively. Pink salmon (*O. gorbuscha*) are taken occasionally in the fisheries, usually in odd years. Each season, the PFMC and the Commission regulate California's ocean salmon fisheries to meet the conservation objectives for Klamath River Fall Chinook (KRFC) and Sacramento River Fall Chinook (SRFC) stocks as described in the Salmon Fishery Management Plan. In addition, the fisheries must meet the NMFS Endangered Species Act consultation standards for listed stocks, including Sacramento winter Chinook (endangered), Central Valley spring Chinook (threatened), California coastal Chinook (threatened), Central California coastal coho (endangered), and Southern Oregon/Northern California coho stocks (threatened).

In 2007, California ocean salmon fisheries were not significantly constrained because both KRFC and SRFC were projected to meet their Salmon FMP conservation objectives. The commercial salmon fishery had 141 more days open than in 2006, primarily in the Fort Bragg area, for a season total of 341 days. In fact, Fort Bragg had its first April commercial fishery (2,000 Chinook quota) since 1979.

An estimated 113,400 Chinook salmon (686 t) were landed during the 2007 commercial season (fig. 8). This was approximately 45% more by weight than the 69,700 salmon (473 t) landed commercially in 2006. The average weight per fish was 6.1 kg (13.3 lbs). The average price was $11.44/kg ($5.19/lb), the highest price on record and just above the $11.27/kg ($5.13/lb, nominal) paid in 2006. The total ex-vessel value of the fishery in 2007 was estimated to be $7.9 million, a 47% increase from the $5.4 million in 2006. Total commercial effort was estimated to be 10,600 boat-days fished, a 28% increase from 8,300 boat-days in 2006.

The 2007 recreational fishing season was considered "wide-open," increased by 90 days compared to the 2006 season, for a season total of 794 days (days open in each of four management areas combined). Regulations permitted two salmon per day of any species except coho. Single-point, single-shank, barbless hooks were required north of Point Conception and anglers fishing with bait and by any means other than trolling were required to use circle hooks. The minimum size limit was 508 mm (20 inches) total length (TL), except in the KMZ where the minimum size limit was 609 mm (24 inches) TL.

An estimated 47,600 Chinook were caught recreationally in 105,700 angler-days in 2007 (fig. 9). This is the lowest harvest and effort observed since CDFG began monitoring in 1962. This represents a 51% decrease in landings and a 16% decrease in effort from 2006. Chinook landed by CPFVs and private skiffs decreased by 65% and 42% respectively compared to 2006.

TABLE 3
Commercial groundfish landings in California for 2007 with comparisons to 2006.

	2007		2006		% change from 2006	% change from 2006
	harvest (m tons)	value ($)	harvest (m tons)	value ($)	(m tons)	($)
Flatfishes						
Dover sole	2,725.4	$2,349,780	1,661.8	$1,359,749	64	73
Petrale sole	887.4	$2,036,153	743.5	$1,697,349	19	20
Rex sole	221.5	$177,506	261.3	$214,204	–15	–17
English sole	175.3	$154,592	256.1	$205,936	–32	–25
Pacific sanddab	152.4	$149,026	118.1	$119,214	29	25
Arrowtooth flounder	59.0	$13,371	39.4	$13,893	50	–4
Starry flounder	13.3	$18,730	20.9	$42,522	–36	–56
Other flatfishes (<1% in '07)	35.3	$66,936	71.0	$112,101	–50	–40
Flatfishes total:	**4,269.6**	**$4,966,094**	**3,172.1**	**$3,764,968**	**35**	**32**
Rockfishes						
Thornyheads	849.3	$2,327,159	892.8	$2,359,041	–5	–1
Splitnose rockfish	72.8	$66,367	125.1	$83,203	–42	–20
Black rockfish	61.7	$264,075	57.5	$231,180	7	14
Blackgill rockfish	55.0	$125,365	82.1	$186,067	–33	–33
Chilipepper	47.0	$82,708	44.8	$67,369	5	23
Bank rockfish	36.4	$79,699	43.4	$78,868	–16	1
Aurora rockfish	35.1	$32,161	25.2	$21,087	39	53
Blue rockfish	29.7	$117,720	22.2	$79,042	34	49
Vermilion rockfish	22.8	$116,891	19.3	$104,562	18	12
Brown rockfish	22.0	$297,023	20.7	$273,829	6	8
Other rockfish (9.3% in '07)	132.8	$1,340,292	115.1	$1,122,279	15	19
Overfished species						
Bocaccio	6.5	$18,371	4.9	$15,845	33	16
Canary rockfish	1.8	$3,304	1.5	$1,880	22	76
Cowcod	2.1	$4,317			N/A	N/A
Darkblotched rockfish	41.4	$54,992	25.9	$30,678	60	79
Pacific ocean perch (POP)	0.5	$552	0.3	$303	106	82
Widow rockfish	8.6	$19,883	8.3	$13,238	4	50
Yelloweye rockfish	0.2	$834	0.0	$6	3660	13800
Rockfishes total:	**1,425.7**	**$4,951,713**	**1,489.0**	**$4,668,477**	**–4**	**6**
Roundfishes						
Pacific whiting	2,986.9	$386,375	5,429.5	$633,197	–45	–39
Sablefish	1,471.6	$4,859,090	1,641.3	$4,894,315	–10	–1
Lingcod	78.4	$255,469	64.3	$196,974	22	30
Cabezon	25.5	$327,809	28.3	$344,600	–10	–5
Kelp greenling	1.5	$20,995	1.6	$23,726	–8	–12
Roundfishes total:	**4,563.9**	**$5,849,738**	**7,165.1**	**$6,092,812**	**–36**	**–4**
Sharks, skates, and rays						
	262.1	$149,772	256.5	$158,659	2	–6
All Groundfish	10,521.3	$15,917,317	12,082.6	$14,684,916	–13	8

Approximately 750 coho were landed illegally during 2007, presumably by anglers who misidentified their salmon as Chinook. This is half the number of coho landed in 2006. It is assumed that many of these fish were part of the mass-marking production of coho currently occurring in Oregon and Washington; half were missing their adipose fin and most did not contain a coded-wire tag (only a small percentage of mass-marked coho contain coded-wire tags).

Fishery managers believe the relatively low commercial and recreational ocean salmon landings were due primarily to a decline in the abundance of SRFC. This stock generally contributes 80–90% of California's ocean landings. In fall 2007, only 88,000 SRFC adults returned to spawn in the Sacramento River basin, which is well below the FMP's conservation goal of 122,000–180,000 adult spawners. In addition, less than 1,900 jacks (age-2 fish) returned (lowest on record). Based on these data, the forecasted ocean abundance for 2008 was approximately 59,000 SRFC, without any additional ocean or in-river fishing. In April 2008, the PFMC and Commission closed all commercial and recreational ocean salmon fishing in California through 30 April 2009 specifically to protect SRFC.

Groundfish

Commercial Fishery Landings. The 10,521 metric tons (t) of commercial groundfish landed in California in 2007 was a 13% decrease from landings in 2006 (12,083 t) (tab. 3), a 2% increase from landings in 2005 (10,347 t), and a 14% decrease from landings in 2004 (12,225 t). Pacific whiting (*Merluccius productus*)

(2,987 t), Dover sole (*Microstomus pacificus*) (2,725 t), and sablefish (*Anoplopoma fimbria*) (1,472 t) continued to be the top species being landed in 2007, identical to species dominating landings in 2004, 2005, and 2006. The Dover sole, thornyheads (*Sebastolobus alascanus* and *S. altivelis*), and sablefish ("DTS" complex) landings accounted for 48% (5,056 t) of all commercial groundfish landings. Overall, roundfishes were caught the most (43%) in 2007, followed by flatfishes (41%) and rockfishes (14%). Overfished rockfish species accounted for less than 1% (61 t) of the landings in 2007, a 49% increase from that in 2006 (41 t). Sharks, skates, and rays accounted for 2% of the total commercial groundfish landings.

The ex-vessel value for commercial groundfish in 2007 was approximately $15.9 million, an 8% increase from 2006 ($14.7 million), and about a 15% increase from 2004 and 2005 (approximately $13.8 million each year). Sablefish is considered the most valuable species being landed, followed by thornyheads, when considering price per metric ton. Again, roundfishes contributed the most to the total ex-vessel value (37%), followed by flatfishes and rockfishes (31% each). Sharks, skates, and rays accounted for only 1% of the total ex-vessel value in 2007.

The majority of groundfish landed were taken by trawl gear (87%), no change from the take of trawl landings in 2006. The remainder was taken with hook-and-line gear (9%), trap gear (3%), and net gear accounted for less than 1% of the total take.

Recreational Fishery Catches. Estimates from the California Recreational Fisheries Survey (CRFS) indicated that in 2007, California anglers targeting bottomfish took an estimated 566,372 angler trips. This was a 34% increase from 2006 (421,104 angler trips). The majority of the effort occurred in southern California (79%), particularly from CPFVs and man-made structures. In northern California (north of Point Conception), about half of the effort was from CPFVs (51%). Private boats accounted for about 20% of the effort, in both the north and the south. No estimates were made for beach and bank effort due to low sample sizes for this mode.

Groundfish take by the recreational fishery was estimated at 1,282 (t) in 2007 (tab. 4), an 18% decrease from 2006 (1,553 t). Even with an increase in effort in 2007, the catch decreased. The species accounting for half of the groundfish catch were vermilion rockfish (*Sebastes miniatus*), lingcod (*Ophiodon elongates*), blue rockfish (*Sebastes mystinus*), and black rockfish (*Sebastes melanops*). The same four species accounted for 61% of the total groundfish catch in 2006. Lingcod was the dominant species caught in the north, followed by black rockfish, blue rockfish, and vermilion rockfish. Vermilion rockfish was the dominant species caught in the south, followed by California scorpionfish (*Scorpaena guttata*), bocaccio (*Sebastes paucispinis*), and copper rockfish (*Sebastes caurinus*). Where the majority of effort was in the south, the north was responsible for catching the most groundfish (71%).

TABLE 4
California recreational groundfish estimates for Examined and Discarded Dead (A+B1) catch by weight (metric tons) in 2007. Note: mortality rates associated with live discards were not incorporated.

Species	Metric Tons	Proportion of total groundfish
Vermilion rockfish	193.0	15%
Lingcod	173.9	14%
Blue rockfish	148.4	12%
Black rockfish	138.2	11%
Copper rockfish	65.9	5%
California scorpionfish	63.8	5%
Brown rockfish	55.7	4%
Yellowtail rockfish	55.6	4%
Olive rockfish	52.1	4%
*Bocaccio	50.9	4%
Gopher rockfish	33.7	3%
Starry rockfish	28.9	2%
Leopard shark	22.0	2%
Cabezon	21.3	2%
Pacific sanddab	15.9	1%
Greenspotted rockfish	13.2	1%
China rockfish	12.6	1%
Quillback rockfish	11.5	1%
Kelp greenling	9.5	1%
Grass rockfish	9.1	1%
Chilipepper	7.8	1%
*Widow rockfish	7.8	1%
Flag rockfish	7.3	1%
Kelp rockfish	7.1	1%
Rockfish genus	34.8	3%
Other	42.0	3%
Total groundfish:	1,282.0	

*Rockfish species of concern. Canary rockfish (5.1 mtons), yelloweye rockfish (3.8 mtons), and cowcod (0.2 mtons) are included in the "other" category.

Blue Rockfish Stock Assessment. Blue rockfish is under joint state-federal management, and in California it is managed under the Nearshore Fishery Management Plan (NFMP). The first blue rockfish stock assessment was completed in 2007 (see http://www.dfg.ca.gov/marine/bluerockfish). This assessment included the blue rockfish stock in California waters north of Point Conception, where blue rockfish are most commonly found. The model used to assess most stocks on the West Coast assumes that a decline in abundance is solely due to fishing, which was not believed to be the case here since declines may be related to environmental conditions, particularly declines in kelp cover. Additional uncertainties of the assessment include the variability in growth of blue rockfish over time and between areas along the coast of California. Genetic evidence has suggested two species of blue rockfish in California waters.

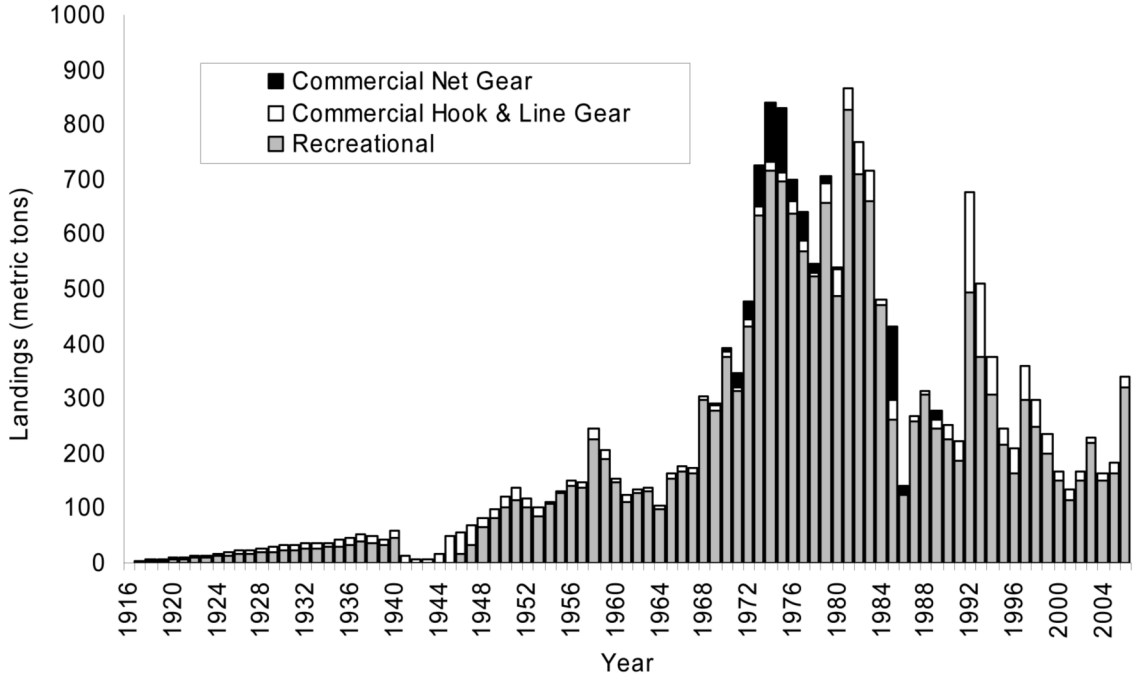

Figure 10. Blue rockfish (*Sebastes mystinus*) landings by gear type in California, north of Point Conception from 1916 to 2006.

Research is needed to determine if there are differences in life-history parameters (i.e., growth, maturity) between the two species that may be essential to appropriately assess the stock. Lastly, a lack of old males in the fishery data was of concern, and could be due to either selectivity (the ability to target and capture fish by size) or a higher natural mortality for males.

Blue rockfish are one of the primary recreationally-caught species in California and are also important in the commercial fishery (mainly hook and line), although landings from the commercial fishery are minor compared to the recreational catch (fig. 10). Due to the lack of historical reporting of blue rockfish catch, a proportion of the early rockfish catch was assigned to blue rockfish, thus the catch history was highly uncertain prior to 1969 in the commercial fishery (non-trawl) and prior to 1980 in the recreational fishery.

Stock Biomass and Recruitment. The model estimated an unfished biomass of 13,223 t, which results in a current depletion level of 29.9% (fig. 11) in 2007, falling just below the NFMP "overfished" threshold of 30%. Considering the uncertainties in the assessment, the stock assessment team felt strongly that the status of the stock was more likely in the range of 30% to 50% of unfished biomass. The highest exploitation rates (and greatest relative population declines) in the 1970s resulted in a continuous decline in spawning biomass through the early 1990s. Recruitment information was limited and highly uncertain for blue rockfish. Recruitment appeared to be high in the 1960s, with all time low recruitment in the late 1970s. More recently, strong year classes appeared in or around 1993 and 1998. Forecasting exercises predict a slight increase in abundance, but not enough to support increased harvesting of blue rockfish in the near future.

Management. The stock assessment for blue rockfish was considered to be data-poor with many uncertainties, which presents challenges to its use for management. Prior to 2000, this species was managed within the *Sebastes* complex, and since then has been managed under the minor nearshore rockfish complex, north and south of Cape Mendocino (40°10'N lat.). In the past, no formal harvest limits were set for blue rockfish. Currently, given the possibility that blue rockfish may be experiencing overfishing, a separate catch limit should be considered, and the catch of blue rockfish should be carefully monitored.

Research and Data Needs. The Stock Assessment Review panel made recommendations on research needs to increase our knowledge of blue rockfish in California and to lessen the uncertainty in the next assessment of this species. These recommendations included better estimates of historic catches, more genetic studies, increased biological sampling and research to provide better insight into life-history parameters, fishery-independent surveys, improving recreational sampling, and an increased understanding of environmental factors affecting survival of juvenile blue rockfish.

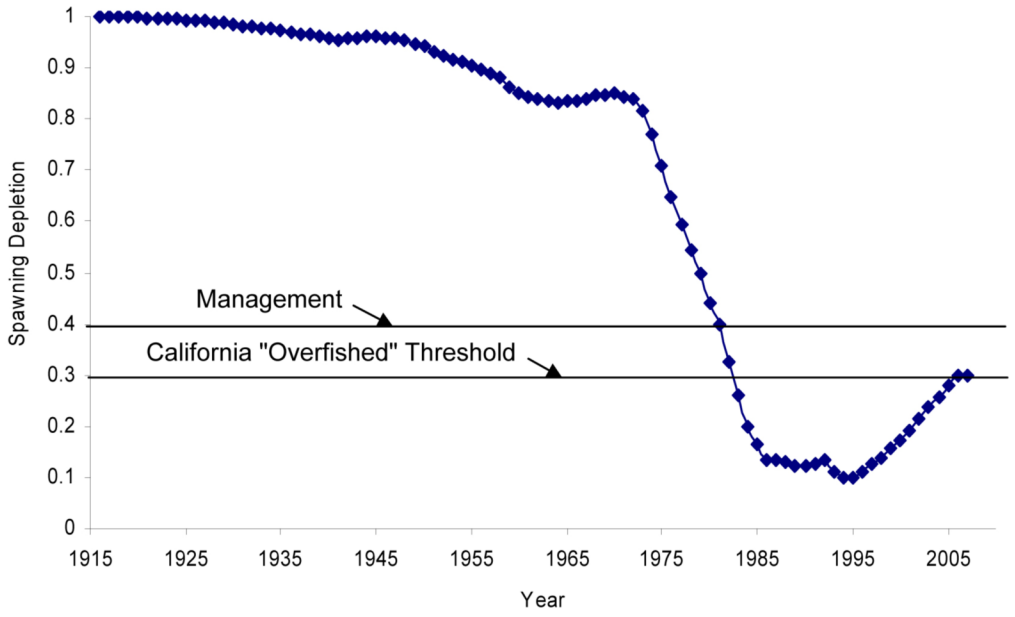

Figure 11. Time series of depletion level for blue rockfish as estimated in the base model. Management target is at 40% of unfished biomass. California's Nearshore Fishery Management Plan (NFMP) defines a stock "overfished" at or below 30% of unfished biomass.

California Halibut

California halibut (*Paralichthys californicus*) is an important flatfish species in both the commercial and recreational fisheries of central and southern California. It is found in nearshore waters on the west coast of North America from Almejas Bay, Baja California Sur, to the Quillayute River, Washington. However, the species is most common south of Bodega Bay, with the center of distribution occurring off northern Baja California. California halibut can reach 1.5 m (5 ft) total length and weigh as much as 33 kg (72 lb).

California halibut is targeted by commercial fisheries using three principal gears: trawl, set gill net, and hook-and-line. Over the past ten years, total annual landings have decreased from a peak of 596 t in 1999 to a low of 174 t in 2007. During this same period, the annual ex-vessel revenue ranged from a high of $3.3 million in 1997 to a low of $1.8 million in 2007.

Since 1916, commercial landings data for California halibut show a periodic shift in the majority of landings between the central and southern California port complexes. Over the past decade, central California ports have received a majority of the landings, except for 2001 and most recently in 2007, when landings were higher in southern California ports. In 2007, the Santa Barbara port complex received 40% of the total landed catch followed by San Francisco (39%), Los Angeles (13%), and San Diego (4%).

Bottom trawl is the most productive commercial gear targeting California halibut. However, landings over the past decade have declined from 331 t in 1998 to a low of 93 t in 2007 (fig. 12). In 2006, a total of 54 trawl vessels landed 228 t of halibut compared to 36 trawl vessels that landed 93 t in 2007; a 59% decrease in landings from the previous year. Regionally, landings in southern California increased by 50% from 2006 landings, while central California landings decreased 71%, due in part to a ban on bottom trawling in Monterey Bay. The San Francisco port complex received 56% of the landings in 2007, followed by Santa Barbara (39%), Los Angeles (2%), and Monterey (2%).

Set gill net landings have also declined in the past decade from a high of 230 t in 1999 to a low of 43 t in 2007. A series of depth restrictions prohibiting set net gear in 60 fathoms or less enacted to protect seabird and sea otter populations along the central California coast have greatly affected the gill net fleet. This is evident by the lack of landings made north of Point Arguello since 2002. A total of 41 gill net vessels landed 47 t in 2006 compared to 40 gill net vessels landing 44 t in 2007. Gill net has become a southern California fishery with the Santa Barbara port complex receiving 54% of 2007 landings, followed by Los Angeles (30%) and San Diego (16%).

Annual landings reported by the hook-and-line fleet have been relatively stable over the past decade, ranging from a high of 99 t in 2003 to a low of 38 t in 2007 (fig. 12). A total of 223 hook-and-line vessels landed 46 t in 2006 compared to 175 vessels that landed 38 t in 2007. Hook-and-line catches by the top three port com-

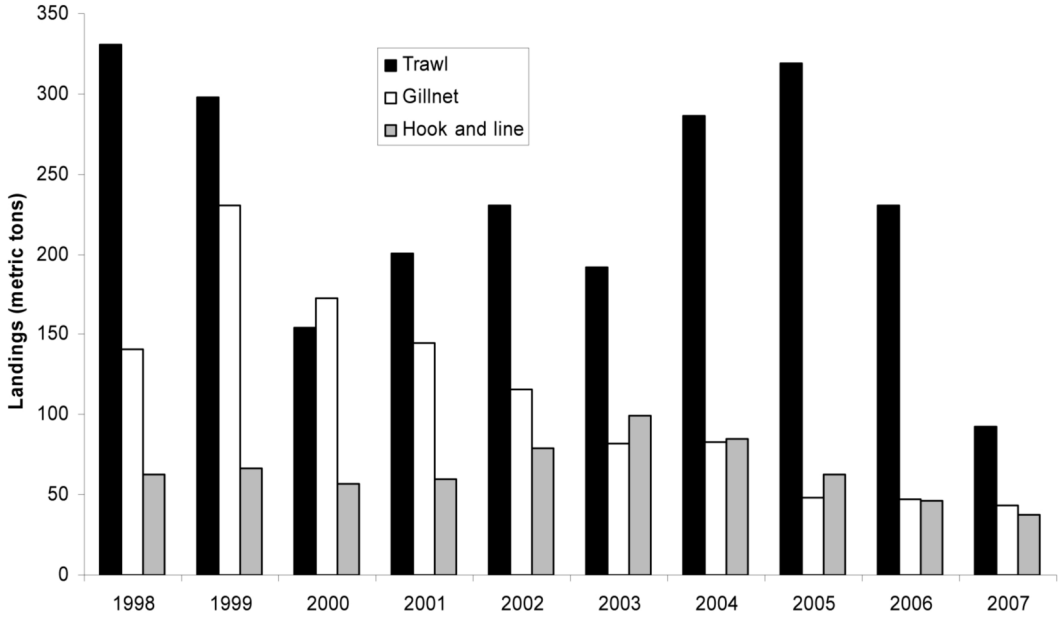

Figure 12. Commercial California halibut (*Paralichthys californicus*) landings by gear type from 1998 to 2007.

plexes were San Francisco (36%), Santa Barbara (28%), and Los Angeles (21%).

The recreational take of halibut, as reported in the Recreational Fisheries Information Network (RecFIN), from the Marine Recreational Fisheries Statistical Survey (MRFSS), showed a significant increase from 429 t (106,000 fish) landed in 1998 to 835 t (199,000 fish) landed in 2003 (fig. 13). Anglers fishing from private and rental boats caught an annual average of 84% of California halibut during this time period. In 2004, the California Recreational Fisheries Survey (CRFS) replaced the MRFSS. Recreational catch estimates obtained from RecFIN show that anglers caught 132 t (35,000 fish) of California halibut statewide in 2007 compared to 133 t (48,000 fish) in 2006 (fig. 14). CRFS data also show that private and rental boats continue to dominate the recreational halibut fishery.

Recent Management Highlights. In 2004, the California Legislature enacted Senate Bill 1459, which added restrictions on bottom trawl gear used in state waters, required implementation of a restricted access program for the California halibut trawl fishery, and granted the Commission management authority over California's bottom trawl fisheries not managed with a state or federal fishery management plan. Additionally, the bill established a timeline for implementing additional closures if certain criteria were not met by the fishery.

A California Halibut Bottom Trawl Vessel Permit program was implemented in 2006. This permit is required for bottom trawling in the designated California Halibut Trawl Grounds (CHTG) located within state waters not less than one nautical mile from shore between Point Arguello (Santa Barbara County) and Point Mugu (Ventura County). Additionally, a permit is required for landings of California halibut in excess of 331 kg (150 lb) that were caught in federal waters. A total of 62 permits were issued in 2006 and 58 permits were renewed in 2007.

In 2005, four areas, which amount to 13% of the CHTG, were closed to trawl gear. In addition, bottom trawling was prohibited within Monterey Bay and additional closures could be implemented in the future if performance criteria were not met. The performance criteria require that the use of trawl gear: (1) minimizes bycatch; (2) is likely not damaging seafloor habitat; (3) is not adversely affecting ecosystem health; and (4) is not impeding reasonable restoration of kelp, coral, or other biogenic habitats. In April 2008, four additional area closures comprising 42% of the CHTG were proposed. However, the Commission made the finding that three of the four should remain open.

Hagfish

The Pacific hagfish (*Eptatretus stoutii*) is a member of the Myxinidae (hagfish) family. Hagfishes are cartilaginous and lack eyes and jaws. They have a single nostril with barbels. Members of this family also have a series of mucus-producing "slime" glands along each side of the body. This mucus, in the presence of water, converts into a jelly-like slime. This slime may act as a defensive mechanism and is produced when hagfish are agitated. Pacific hagfish occur in depths from 9 to 732 m with a

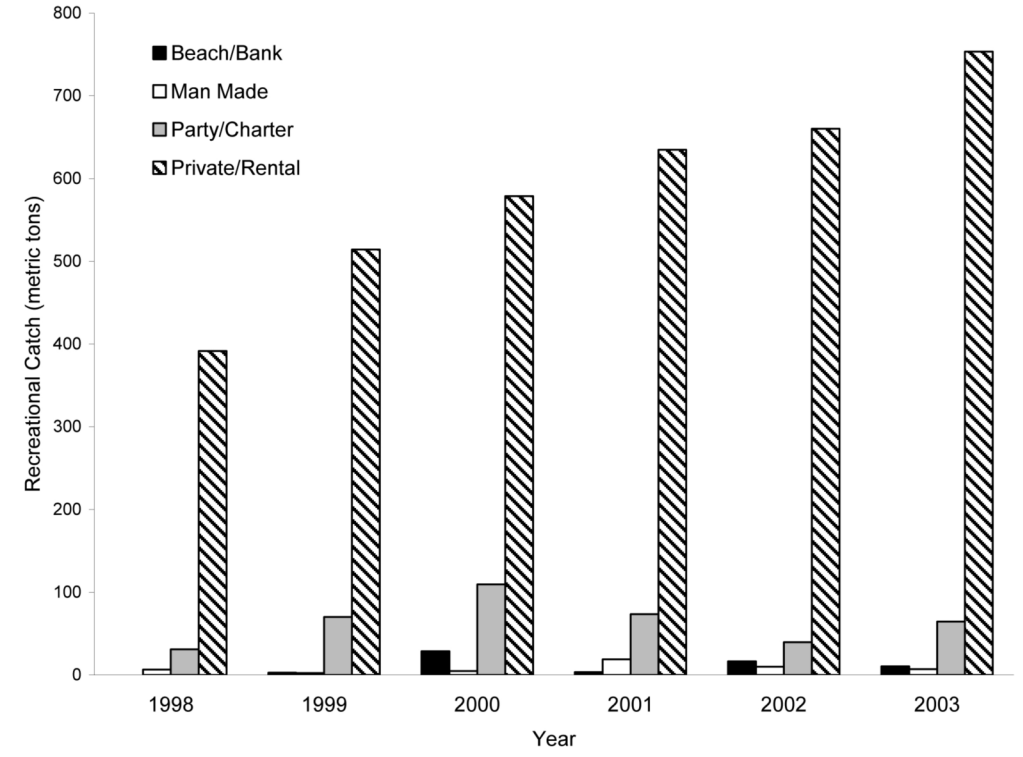

Figure 13. Recreational landings of California halibut, (*Paralichthys californicus*) as reported in the Marine Recreational Fisheries Statistical Survey (MRFSS), by four different fishing modes, from 1998 to 2003.

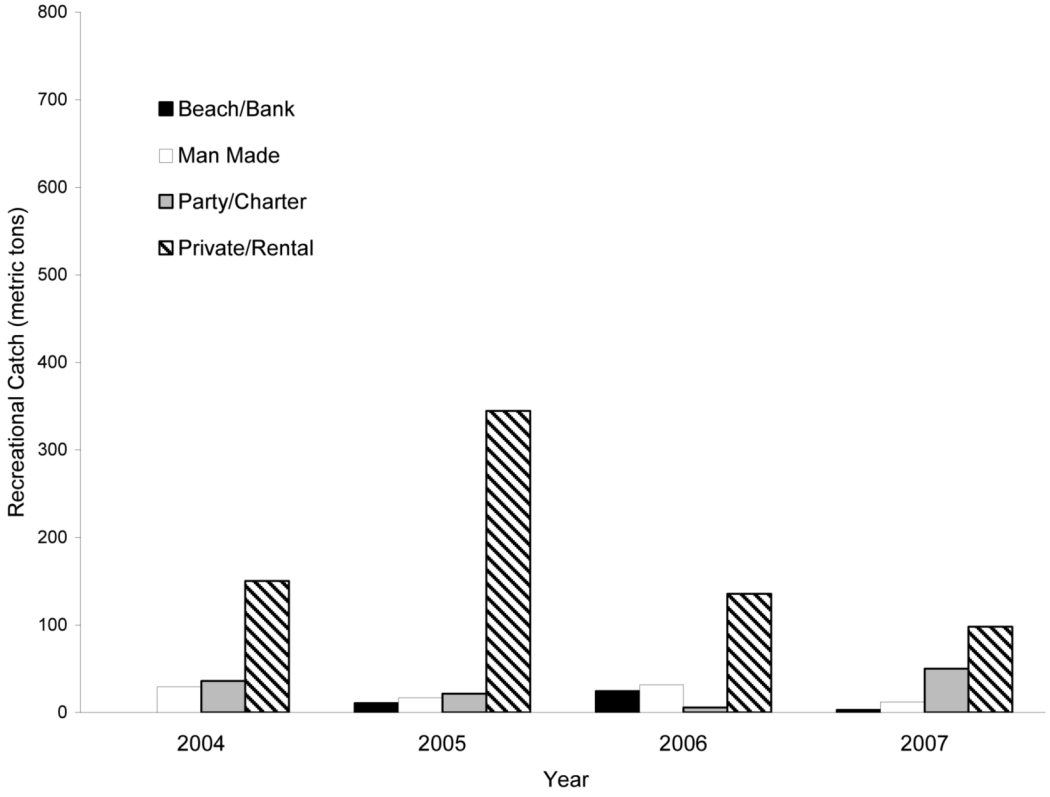

Figure 14. Recreational landings of California halibut, (*Paralichthys californicus*) as reported in the California Recreational Fisheries Survey (CRFS), by four different fishing modes, from 2004 to 2007.

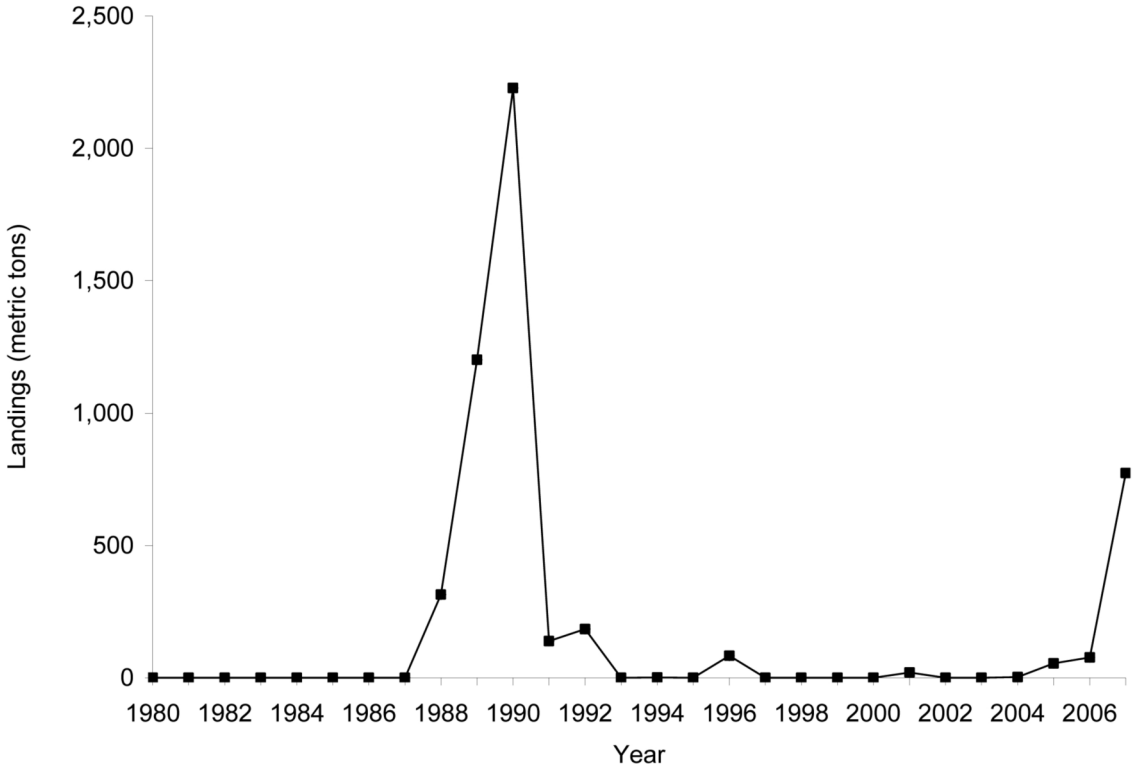

Figure 15. California commercial landings of Pacific hagfish (*Eptatretus stoutii*) from 1980 to 2007.

preference for muddy substrate. Considered scavengers, hagfish will feed upon dead fish and marine mammals, or any other animal matter they can find. Knowledge of maturation and fecundity is limited, although studies indicate that females attain sexual maturity around 325 mm total length and are between 7 and 12 years old. Hagfish fecundity is low with a female hagfish producing 20–30 eggs per reproductive cycle. Viable female hagfish may contain eggs of various stages of maturity. Reproductive cycle length is not known; however, a female's eggs must come to full term before the next batch of eggs will mature.

Prior to 1988, hagfish landings in California were nonexistent (fig. 15). Hagfish were considered an undesirable species by U.S. fishermen but were in great demand in South Korea. Their skins are used to manufacture wallets and they are now considered a sushi delicacy for human consumption. Localized depletion of related species, brown hagfish (*Paramyxine atami*) and inshore hagfish (*Eptatretus burgeri*), near South Korea increased demand for imported hagfish from the United States in the late 1980s. In 1988, fishermen from San Francisco and Monterey were recruited to harvest hagfish for one Korean buyer. Landings and fishing effort expanded in 1989 leading to 1,201 t of hagfish landed statewide. By 1990, hagfish were landed from Eureka to San Diego. Total landings for 1990 were 2,228 t, the highest annual landings on record. Most exported hagfish were landed fresh and then frozen for use in the Korean leather goods market. Due to Korean processing laws, imported hagfish could only be used for their skin and the flesh was discarded. While total landings increased between 1989 and 1990, Korean demand for California-caught hagfish began to decrease due to quality of skins. Hagfish from California were less desirable than those from British Columbia due to unexplained blemishes and holes.

By 2005, hagfish were no longer exported for their skin, but rather for human consumption, and were sold primarily in a live condition. In addition to a resurgence in Korean demand, many displaced commercial fishermen were looking for other sources of income. In 2007, total landings increased sharply to 773 t and ex-vessel price ranged between $0.22/kg and $3.97/kg with an average of $0.70/kg. Once again, hagfish were landed from Eureka to San Diego with 62% of the 2007 landings from Eureka, followed by Monterey (16%), Los Angeles (15%), and Santa Barbara (7%). By early 2008, ex-vessel price ranged between $0.55/kg and $4.41/kg and averaged $1.73/kg. The higher prices are realized for live fish.

Hagfish are taken commercially using bucket traps or Korean traps primarily in the depth range of 55 to 185 m, although fishing occurs out to 370 m. There is no recreational fishery for hagfish. Bucket traps are constructed

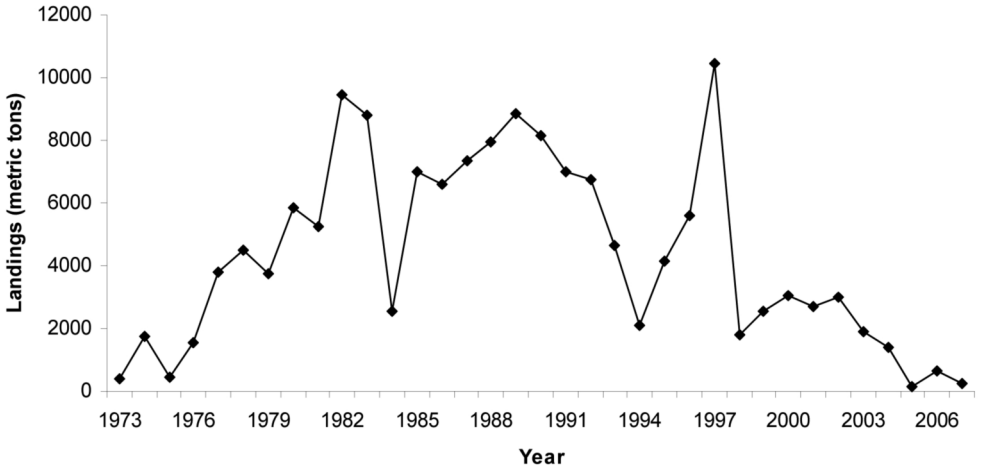

Figure 16. San Francisco Bay commercial Pacific herring (*Clupea pallasi*) sac roe landings from 1972 to 2007.

using a five-gallon bucket drilled with holes to allow water flow. A self-closing plastic cone acts as the door. Bucket traps are fished in a string with a single marker float. Korean traps are elongated plastic cylinders no greater than 15.24 cm in diameter and no more than 60.96 cm long. Korean traps employ the same type of plastic cone for an entrance. Vessels are limited to 500 Korean traps or 200 bucket traps. No species other than Pacific hagfish can be taken, possessed, or sold when Korean or bucket traps are on board the vessel. All traps must have a destruct device and popups (time-released buoys) are prohibited. A general trap permit is required to participate in this open access fishery. Traps are baited with anchovies, sardines, mackerel, squid, or fish carcasses. In 2007, the Department began to actively monitor hagfish fishing activity. Due to the difficulty in measuring live hagfish, an average count per kg per observed landing is used to document changes in average size of landed hagfish.

Pacific Herring

California's Pacific herring (*Clupea pallasi*) fisheries in 2007 had the second lowest landings in the 35-year history of the modern fishery. Statewide landings for the 2006–07 sac roe season (December 2006–March 2007) totaled 266 t, with permittees not reaching their quotas in any embayment. The San Francisco Bay fleet landed 264.9 t, 39% of their 2005–06 landings (674.9 t) (fig. 16), and only 6.7% of the 3,926 t quota. The Tomales fleet landed 1.1 t, only 0.3% of their 318 t quota and no herring were landed the previous season. Data from herring population studies conducted in San Francisco Bay suggest that fish are smaller at age, which may make them less available to commercial gill nets. There was no fishing effort in Humboldt Bay or Crescent City Harbor during the 2006–07 season.

The forecast base price for roe herring is a good indicator of the economic status of the fishery, and a factor in whether fishermen will participate in the fishery. Ex-vessel prices for roe herring are determined by a set base price, and an additional roe percentage point bonus. The base price is set per short ton of roe herring with a minimum roe percentage of 10%. Roe herring that are landed, which exceed the minimum roe recovery level, are given a bonus for each percentage point exceeding 10%. Ex-vessel prices in the herring sac roe fishery can vary greatly based on roe recovery rates. The 2006–07 ex-vessel prices for roe herring with 10% or greater roe recovery was $400 per short ton landed, with an additional $40 paid for each percentage point above the 10% baseline. The average roe count for the 2006–07 season was 16%, resulting in an ex-vessel value of $640 per short ton. Due to a decrease in landings, the statewide ex-vessel value of the herring sac roe fishery fell from $426,408 in 2006 to $187,461 in 2007.

The San Francisco Bay herring eggs-on-kelp fishery landed 8.5 t, 28% of their 30.8 t quota, whereas the previous season had no fishing activity. Price paid for eggs-on-kelp ranges from $13.2–39.6/kg ($6–18/lb) depending on the quality of the product. The total estimated value of the 2006–07 eggs-on-kelp harvest was approximately $162,996 based on an average ex-vessel price of $19.1/kg ($8.67/lb).

CDFG conducted spawn deposition surveys in San Francisco and Humboldt Bays to estimate the spawning biomass of the herring stock. The 2006–07 spawning biomass estimate for San Francisco Bay was 9,924 t, a 92% decrease from last season's estimate of 131,591 t. This estimate is the lowest recorded estimate in the history of the roe herring fishery, from the 1978–79 season to present. The precipitous drop in spawning biomass from a record high in 2005–06 to a record low in

2006–07 may have been caused by unfavorable environmental conditions associated with an El Niño event and an unusually dry winter. The spawning biomass estimate in Humboldt Bay for 2006–07 season was 6.4 t. This was the lowest biomass estimate recorded in the 11 seasons of spawn assessment surveys conducted in Humboldt Bay, and is just a fraction of the 11-year average of 331 t. No spawning biomass estimates were made for Tomales Bay or Crescent City in 2007.

The decline in value of California's herring fisheries is related to cultural and demographic changes in Japan, the status of Japan's economy, and increased competition from other herring fisheries outside of California. The herring roe product, "kazunoko," remains a popular Japanese New Year's food, but it continues to wane as a traditional holiday gift. The market for herring sac roe in Japan is shifting from a high-end seasonal gift product to a lower-value product geared toward the casual consumer that is available throughout the year. California's roe herring fishery faces competition in the Japanese market with products from other herring fisheries from the United States, Canada, China, and Russia.

Recreational Fishery

In 2007, CDFG received 29,497 logs from 307 CPFVs which carry sport fishing anglers and divers for hire in ocean waters off the coast of California. Of the 307 vessels submitting logs to CDFG, two split their fishing time between northern and southern California.

Since 1936, CPFV owners and operators have been required by law to submit a log of daily fishing activities. This long-term data series provides the Department with important information on catch trends and effort in recreational fishing. Fishing from CPFVs is just one component of the entire spectrum of recreational fishing that occurs. To monitor the full scope of California's recreational fishery resources, the CRFS was implemented in 2004 to collect data through field sampling and telephone surveys on all modes of recreational fishing (CPFVs, private vessels, piers, banks, and shorelines), with the primary goal of producing, in a timely manner, data needed to sustainably manage California's marine recreational fishery resources. In the future, CDFG hopes to incorporate the CPFV effort data from logbooks into the CRFS program.

Southern California. Anglers on CPFVs originating in southern California, fishing from Point Conception to the waters off Baja California, Mexico, have traditionally targeted a variety of fish species, while divers have historically targeted invertebrates such as California spiny lobster and rock scallop (*Crassadoma gigantean*) on the CPFV dive boats in southern California. The species being targeted can vary with season and year. Occasionally in waters off southern California, ENSO conditions greatly increase the availability of species normally found in warmer waters off Mexico. Conversely, La Niña conditions increase the availability of colder-water species. Operators of CPFVs are typically quick to take advantage of the fishing opportunities provided by these changing oceanographic conditions.

In 2007, 435,821 anglers aboard 203 reporting CPFVs caught 1,974,394 fish and invertebrates south of Point Conception to waters off of Baja California (tab. 5). The catch kept by anglers in southern California in 2007 decreased by 8% compared to 2006 and the number of anglers fishing from CPFVs dropped by 6% in 2007 compared to 2006. The southern California anglers represented 80% of the anglers fishing from CPFVs statewide and caught 73% of the statewide total number of fish in 2007.

The southern California top-ten fish species or species groups reported on CPFV logs in 2007 (by number of fish kept) were rockfish (all species combined) (*Sebastes* spp.), kelp bass (*Paralabrax clathratus*), California scorpionfish, barred sand bass (*Paralabrax nebulifer*), California barracuda (*Sphyraena argentea*), sanddab (all species combined) (*Citharichthys* spp.), albacore tuna, ocean whitefish (*Caulolatilus princeps*), yellowtail (*Seriola lalandi*), and halfmoon (*Medialuna californiensis*). These top-ten species or species groups included nine of the top ten groups from 2006. The one exception was albacore tuna, which was ranked number 15 in 2006 and moved up to rank 7 in 2007. The order of abundance also changed for eight of the top-ten species or species groups between 2007 and 2006, except for rockfishes (all species combined), which remained number one for both years, and halfmoon that ranked number ten in both years (tab. 5).

For the top-twenty species of fish, catch, as reported on CPFV logs, decreased in 2007 compared to 2006 for kelp bass, barred sand bass, yellowtail, Pacific bonito, Pacific mackerel, California sheephead (*Semicossyphus pulcher*), yellowfin tuna, dorado (dolphinfish), unspecified perch-like fish (Kyphosidae/Pomacentridae), California halibut, and wahoo (*Acanthocybium solanderi*) (tab. 5). Decreases in some of the more southern highly migratory species (e.g., yellowtail, yellowfin tuna, dolphinfish) can be attributed primarily to decreased availability. Cooler oceanic waters moved onshore along the California coast in early 2007, shifting the spring and summer distribution of some of these species southward. Decreased catch of Pacific mackerel and Pacific bonito also may have been related to decreased availability.

In response to the decreased availability of warmer-water species in 2007, the southern California CPFV operators shifted their efforts to other species or species groups, including albacore tuna, California barracuda, sanddabs, and a number of nearshore species (tab. 5). Albacore landings increased almost five-fold compared

TABLE 5
Southern California Commericial Passenger Fishing Vessel (CPFV) Catch (Number of Fish) in 2007 and 2006.

Species/Species Group	2007 Catch No. of fish	Rank	% change from 2006	2006 Catch No. of fish	Rank
Rockfish (all species combined)	492,492	1	+5	470,416	1
Kelp bass	226,997	2	–15	267,144	3
California scorpionfish	203,151	3	0	203,504	5
Barred sand bass	187,130	4	–32	277,165	2
California barracuda	169,204	5	+48	114,416	7
Sanddab	102,356	6	+38	74,059	8
Albacore tuna	96,736	7	+383	20,045	15
Ocean whitefish	80,753	8	+30	62,132	9
Yellowtail	78,078	9	–55	173,320	6
Halfmoon	59,814	10	+7	55,806	10
Pacific bonito	59,439	11	–71	204,793	4
Pacific mackerel	34,899	12	–8	37,933	13
California sheephead	29,775	13	–4	31,129	14
Yellowfin tuna	16,140	14	–66	46,919	11
Lingcod	9,317	15	+4	8,216	17
Blacksmith	7,180	16	+80	3,999	21
Dorado (dolphinfish)	5,646	17	–88	46,122	11
Perch-like, unspecified*	4,268	18	–50	8,488	16
Halibut-California	2,198	19	–22	2,808	23
Wahoo	2,193	20	–41	3,722	22
Fishes, unspecified**	11,199		–59	27,347	
Sharks/Rays, unspecified**	300		–33	450	
Invertebrates, unspecified**	1,380		+1280	100	
Invertebrates (lobster/scallop)	18,075		+4	17,355	
Jumbo squid	75,674		+47,795	158	
Total number kept	1,974,394		–8	2,157,546	
Number of anglers	435,821		–6	464,989	
Reporting CPFVs	211		–5	223	

*Unspecified by CPFV skipper
**Unspecified by the author

TABLE 6
Top Ten Rockfish Species Catch (Number of Fish) from Southern California CPFVs in 2007 and 2006.

Species/Species Group	2007 Catch No. of fish	Rank	% change from 2006	2006 Catch No. of fish	Rank
Rockfish, unspecified*	373,640	1	+6	353,574	1
Bocaccio rockfish	50,192	2	+25	40,208	2
Copper rockfish	27,934	3	+4	26,878	4
Blue rockfish	18,859	4	–35	28,929	3
Red group rockfish*	7,668	5	–7	8,248	5
Widow rockfish	5,522	6	+97	2,810	8
Gopher rockfish	4,799	7	+44	3,340	7
Vermilion rockfish	1,596	8	–67	4,865	6
Canary rockfish	1,234	9	+536	194	10
Yelloweye rockfish	324	10	+449	59	14

*Unspecified by CPFV skipper

to 2006, while California barracuda and sanddab landings increased by 48% and 38%, respectively. Increased catch was also reported for a number of nearshore species including ocean whitefish, halfmoon, lingcod, blacksmith (*Chromis punctipinnis*), and various rockfish species.

Total rockfish catch increased 5% between 2007 and 2006 (tab. 5). Seven of the ten rockfish species or species groups showed an increase between 2007 and 2006 (tab. 6). Although retention of canary rockfish (*Sebastes pinniger*) and yelloweye rockfish (*S. ruberrimus*) has been prohibited since 2002, some were reported kept in 2007. The number of blue rockfish and vermilion rockfish reported kept decreased by 35% and 67%, respectively, between 2006 and 2007.

Jumbo squid (*Dosidicus gigas*) first showed up in CPFV catches in large quantities off Monterey, California, during the El Niño year of 1997. Anglers found these large squid could be caught on standard hook-and-line gear and an opportunistic fishery developed dependent on the availability of this invertebrate species.

An ENSO event was predicted for late 2006 into early 2007, but it was weak and dissipated early. This event

TABLE 7
Central and Northern California CPFV Catch (Number of Fish) in 2007 and 2006.

Species/Species Group	2007 Catch No. of fish	Rank	% change from 2006	2006 Catch No. of fish	Rank
Rockfish (all species combined)	610,635	1	–9	670,814	1
Sanddab	23,930	2	–3	24,791	4
Lingcod	15,355	3	–44	27,424	3
Chinook salmon***	12,300	4	–65	35,300	2
Pacific mackerel	11,487	5	–5	12,054	5
Striped bass	5,936	6	+127	2,614	9
California halibut	3,520	7	+13	3,116	7
Kelp greenling	2,246	8	–3	2,310	10
Albacore tuna	1,838	9	+89	975	12
Cabezon	1,180	10	–12	1,339	11
Fishes, unspecified**	1,705	–78	7,601		
Sharks/Rays, unspecified**	647	–53	1,370		
Invertebrates, unspecified**	160	–41	273		
Dungeness crab	25,024	–35	38,513		
Jumbo squid	6,546	–54	14,211		
Total number kept	722,509	–14	842,705		
Number of anglers	107,036	–11	120,315		
Reporting CPFVs	114	–2	116		

**Unspecified by the author
***Catch numbers provided by Ocean Salmon Project

may have caused an influx of warm water from the south to bring the jumbo squid into central and northern California waters in 2006. They then may have moved south in 2007 as the warm-water mass dissipated. Jumbo squid movement patterns are highly variable in space and time, making it difficult to predict their availability in any given year. In 2007, 75,674 jumbo squid were caught by anglers aboard CPFVs operating in the Los Angeles area and south, compared to 158 reported in 2006 (tab. 5). While the 2007 catch was substantially higher than the catch in 2006, it was still well below the catches in 1999 and 2002 when 119,164 and 198,364, respectively, were caught.

Central and Northern California. Along the California coast north of Point Conception to the California-Oregon border, CPFV anglers traditionally target rockfish, salmon, lingcod, and, opportunistically, albacore tuna. Cabezon and other nearshore species are also taken. California halibut, striped bass, sturgeon, and leopard shark are primarily taken from within San Francisco Bay. In addition, more southerly species such as bluefin tuna, white seabass, skipjack tuna, and yellowtail may be targeted in warm-water years.

In 2007, 107,036 anglers aboard 106 reporting CPFVs caught 722,509 fish and invertebrates north of Point Conception, a 14% decrease from 2006 (tab. 7). The decrease in the catch kept between 2007 and 2006 was in part due to unexpectedly low returns of Chinook salmon, decreased availability of Dungeness crab due to natural population fluctuations, an early closure of the rockfish and lingcod fishery in parts of northern California on 1 October 2007, and the movement of jumbo squid out of the area. The central and northern California kept fish accounted for 27% of the state's total catch (2,696,903). Central and northern California anglers represented 20% of the anglers fishing from CPFVs statewide.

The top-ten species or species groups in 2007 reported kept by anglers aboard central and northern California CPFVs (by number of fish) were rockfishes (all species combined), sanddab (all species combined), lingcod, Chinook salmon, Pacific mackerel, striped bass (*Morone saxatilus*), California halibut, kelp greenling (*Hexagrammos decagrammus*), albacore tuna, and cabezon (*Scorpaenichthys marmoratus*) (tab. 7). The top-ten species or species groups included eight of the top ten from 2006. The exceptions were albacore tuna catch, which increased 89% between 2007 and 2006, and cabezon, which decreased by 12%, but still moved from rank 11 in 2006 to rank 10 in 2007.

Most of the other top-ten species or species groups and invertebrates reported a decline in the number of fish kept in 2007 compared to 2006, except striped bass and California halibut, which increased 127% and 13%, respectively. Total rockfish catch decreased 9% between 2007 and 2006, with 610,635 and 670,814 fish kept, respectively. Most of the rankings of the other top-ten species and species groups changed between 2007 and 2006. The number of invertebrates kept in 2007 in northern and central California decreased significantly, with Dungeness crab dropping 35% from 38,513 in 2006 to 25,024 in 2007, and jumbo squid dropping 54% from 14,211 in 2006 to 6,546 in 2007 (tab. 7). This is in contrast to the reported catch of invertebrates in southern California, where the number of jumbo squid reported

TABLE 8
Top Ten Rockfish Species Catch (Number of Fish) from Central and Northern California CPFVs in 2007 and 2006.

Species/Species Group	2007 Catch No. of fish	Rank	% change from 2006	2006 Catch No. of fish	Rank
Rockfish, unspecified*	211,542	1	+22	172,695	2
Blue rockfish	202,751	2	–32	298,974	1
Black rockfish	65,561	3	+8	60,898	3
Gopher rockfish	30,936	4	+23	25,192	5
Vermilion rockfish	30,444	5	–16	36,367	4
Copper rockfish	20,279	6	+5	19,223	6
Widow rockfish	15,020	7	–9	16,581	8
Brown rockfish	11,074	8	–16	13,229	9
Red group rockfish*	10,351	9	–39	16,992	7
Bocaccio rockfish	7,090	10	–14	8,250	10

*Unspecified by CPFV skipper

kept increased tremendously between 2006 and 2007 and the number of California spiny lobster and rock scallop reported kept increased in 2007 (tabs. 5, 7). Six of the ten species or species groups showed a decrease in catch between 2007 and 2006 (tab. 7). The two with the greatest declines were the unspecified red group rockfish (39%) and blue rockfish whose 32% decrease in the number of fish kept in the central and northern California area was similar to the 35% decrease reported for the southern part of the state (tab. 8). By contrast, two species or species groups reported increased catch in 2007 compared to 2006: the unspecified rockfish category increased 22% and gopher rockfish (*Sebastes carnatus*) increased 23%.

The number of Chinook salmon reported kept in 2007 decreased by 65% compared to 2006 (tab. 7). Fishery managers believe this decrease was primarily due to the decline of SRFC, which usually contributes significantly (80–90%) to California's ocean sport catch.

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THE STATE OF THE CALIFORNIA CURRENT, 2007–2008: LA NIÑA CONDITIONS AND THEIR EFFECTS ON THE ECOSYSTEM

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ABSTRACT

The state of the California Current system (CCS) between Oregon and Baja California is summarized in this report, covering spring of 2007 to winter/spring 2008. The 2006–07 period began with moderate El Niño conditions which decayed rapidly in early 2007. By summer 2007, a moderate-to-strong La Niña had developed. The North Pacific sea surface temperature (SST) anomalies displayed a negative pattern of Pacific Decadal Oscillation with below-normal SSTs in the California Current and Gulf of Alaska consistent with this pattern. The region experienced anomalously strong southward coastal winds, leading to positive anomalies of the West Coast upwelling index, in strong contrast with 2005. The 2007 upwelling season also began early (in contrast to delayed onset in 2005 and 2006) and remained unseasonably strong through May. The cumulative upwelling for the 2007 season was greater than normal in the southern portion of the California Current system. Despite the La Niña conditions, nitrate and chlorophyll concentrations off Oregon were about average in 2007. On the other hand, copepod biomass rebounded strongly in 2006 after the exceptionally low biomass in 2005, and copepod species richness in 2006 was low, also indicating transport of sub-arctic water into the northern California Current in 2006–07, which is relatively productive but low in diversity.

Anomalously high salinities at 200 m depth were also observed during CalCOFI and IMECOCAL cruises off southern and Baja California. In the CalCOFI area, where there has been a general trend toward a deepening mixed layer, the mixed layer responded to this year's La Niña conditions by shoaling. Nitrate (but not silicate and phosphate) concentrations in the mixed layer were anomalously high, but chlorophyll concentrations were about average, except for spring 2007, which was one of the lowest values on record. Spring chlorophyll *a* concentrations are notably variable during La Niñas. In the northern California Current, forage fish and predatory fish abundance remained low in 2007. In the southern California Current, Pacific sardine (*Sardinops sagax*) larval abundance was relatively high and distributed in relation to the inner edge of the California Current and the edge of an eddy. Northern anchovy (*Engraulis mordax*) larvae were relatively low in abundance, apparently related to a large downwelling feature. Reproductive success of all six seabirds monitored on Farallon Island was recovering slowly this year, following the previous two disastrous seasons. However, cluster analysis indicated that reproductive success is still relatively low. The cold-water planktivorous auklets (*Ptychoramphus aleuticus*) continued to be found at high densities in southern waters.

Overall, the transition in 2007 to La Niña conditions appeared to contribute to average to above average pro-

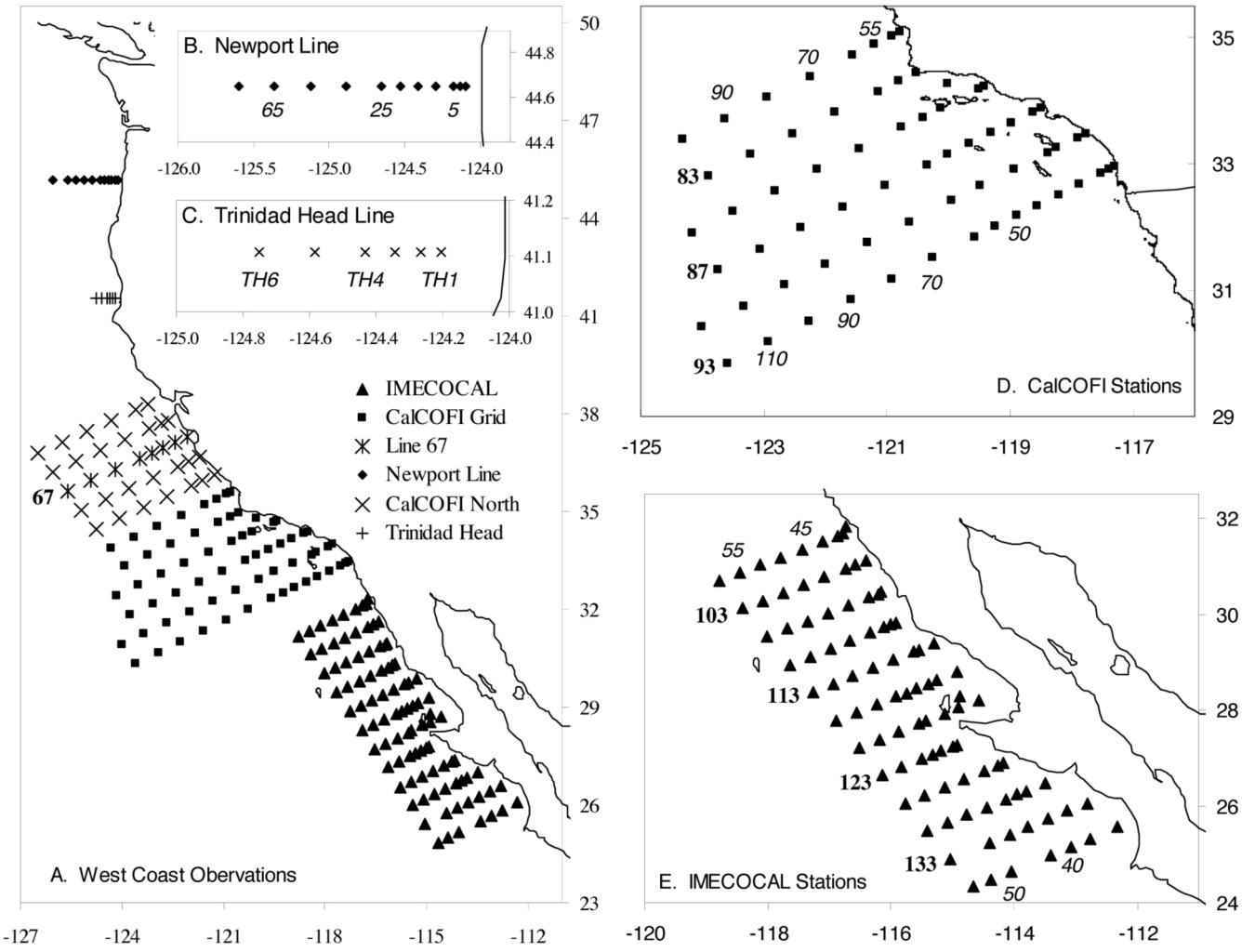

Figure 1. Location of stations where observations were made for this year's report. Observational lines are labeled using bold numbers positioned west of the line terminus; stations are labeled using numbers in italics immediately below or above the respective stations. Line and station numbers for the IMECOCAL and CalCOFI programs are following the CalCOFI line and station nomenclature. The IMECOCAL program covers all lines out to station 60, i.e., the westernmost station on any IMECOCAL line is 60. The CalCOFI program is covering lines 93 and 90 out to station 120, lines 87 and 83 to station 110 and lines 80 and 77 to lines 100. The Newport Line station names designate distance (nm) from shore. The 66 standard CalCOFI stations (black squares in A) are occupied on all cruises, weather permitting. During the winter and spring cruises the pattern is extended north for observations of hydrographic properties and distributions of fish eggs and larvae (crosses). The Monterey Bay Aquarium Research Institute monitors conditions in Monterey Bay triweekly and, with the Naval Postgraduate School and UCSC, occupies CaCOFI lines 67 and 60 westward to station 90 quarterly. The Newport line is covered biweekly out to St. 25 and occasionally farther offshore. The Trinidad Head line is covered monthly. The Newport line is covered biweekly out to St. 25 and occasionally farther offshore.

ductivity in the California Current, but the physical, chemical, and biological (phytoplankton, zooplankton, fish, and seabird) indices of productivity were far from consistent.

INTRODUCTION

This report summarizes the climatology, oceanography, and biology of the California Current system (CCS) between the spring of 2007 and the spring of 2008. It is based on observations taken between Oregon and Baja California. Participating programs or institutions include the NOAA Fisheries Pacific Fisheries Environmental Laboratory (PFEL) providing basin- and coast-wide climatologies, the NOAA Fisheries Stock Assessment Improvement Program working off Oregon, the Point Reyes Bird Observatory (PRBO) studying seabirds off central and southern California, the CalCOFI program working off southern California, and the Investigaciones Mexicanas de la Corriente de California program (IMECOCAL) working off Baja California, and a collaborative effort between the NOAA Fisheries Southwest Fishery Science Center Fisheries Ecology Division and Humboldt State University to collect ocean observations off northern California. The stations regularly occupied by these programs are shown in Figure 1. The objective of this report is to describe the state of the CCS over

the last year, to compare this to long-term conditions, and to relate changes of the state of the ecosystem to forcing by climate. In a report of this nature it is not possible to provide all substantiating data for each statement, and the reader is encouraged to seek more detailed analyses in other more narrowly focused publications.

Over the last decade the north Pacific Ocean has been in a cool phase characterized by negative or neutral values of the Pacific Decadal Oscillation (PDO) index and associated large negative sea surface temperature (SST) anomalies throughout the California Current system. The ecosystem responded to this forcing (Bograd et al. 2000; Peterson and Schwing 2003) with increased zooplankton production and, at times, dramatic shifts in community structure (Brinton and Townsend 2003; Lavaniegos and Ohman 2003). A weak equatorial El Niño/Southern Oscillation (ENSO) event in 2002–03 had only small effects on the California Current system (Venrick et al. 2003). Over the last four years regional or local forcing dominated hydrographic properties and the ecosystem's response. Notable events during this time period were the late onset of upwelling off Oregon and central California in 2005 and 2006 (Petersen et al. 2006; Goericke et al. 2007), with dramatic consequences for the ecosystem, e.g., the almost zero reproductive success of some seabird species on the Farallon Islands (Sydeman et al. 2006; Goericke et al. 2007). The intrusion of cold and fresh waters into the upper 200 m of the CCS, which lasted from 2003 to 2007, had dramatic effects on nutrients and concentrations of chlorophyll *a* off Oregon but only moderate effects on hydrographic properties and negligible effects on the ecosystem off southern California and Baja California (Venrick et al. 2003).

It is important to determine to what extent the CCS is affected by global climate change. Even though it is in most cases not possible to attribute regional long-term changes, such as changes of SST or changes of deep hydrographic properties in the different areas (e.g., the CalCOFI study region, Goericke et al. 2007) to global climate changes, disproving this hypothesis is equally difficult. Nevertheless, we need to view data with global climate change in mind and ask how changes in key system variables—temperature, nutrient supply rates, atmospheric forcing—will affect ecosystem structure and function.

During the time this report covers, i.e., the year 2007 and the winter and spring of 2008, the north Pacific Ocean experienced strong La Niña conditions that dominated forcing throughout the CCS (see below). This report will focus on describing the response of the CCS to this forcing. In particular we will discuss how the ecosystem responded to the cooling of the surface ocean during this period and contrast it with other similar events, the 1988–89 La Niña that occurred during a period of positive PDO index values, and the extended 1999–2000 La Niña that coincided with the transition of the CCS into a cold phase.

DATA SETS AND METHODS

Large-Scale Analyses

Large-scale patterns are summarized from the National Center for Environmental Prediction reanalysis fields (Kistler et al. 2001) and from the NOAA-CIRES climate Diagnostics Center (http://www.cdc.noaa.gov/). The reanalysis fields are monthly gridded (approximately 2° x 2°) anomalies of sea surface temperature (SST) and surface winds. The base period is 1968–96. Monthly upwelling indices and their anomalies for the North American west coast (21°–52° N) are calculated relative to 1948–67. The daily along-shore wind component and SST are from the NOAA National Data Buoy Center (NDBC). Values from six representative buoys from the CCS are plotted against the harmonic mean of each buoy.

Regional Analyses—Oregon

Regular sampling of the Newport Hydrographic (NH) line along 44.65°N continues on a biweekly basis along the inner portions of the line, at seven stations ranging from 1 to 25 nautical miles from shore. Methods and measurements are the same as listed in last year's report (Peterson et al. 2006).

Since 1998, pelagic forage and predatory fish have been sampled every ten nights from mid-April through mid-July. Four stations are occupied along each of two transects off the Columbia River and southern Washington. At each station, a 30 minute pelagic rope trawl is towed between the surface and 20 m. Additional details may be found in last year's report.

Regional Analyses—Northern California

An ocean observing effort has been recently established by NOAA's National Marine Fisheries Service (NMFS) in cooperation with Humboldt State University. Data are collected at roughly monthly intervals along the Trinidad Head line (41°31.5'N), which consists of six stations along a transect extending approximately 50 km due west from Trinidad Head (fig. 1). At each station, a conductivity-temperature-depth (CTD) cast to 150 m (or as limited by bathymetry) is performed to collect data on temperature (T), salinity (S), dissolved oxygen, fluorescence, and transmissivity. Plankton are sampled by (1) an oblique tow from a maximum of 100 m depth with a 70 cm bongo frame fitted with dyed 505 μm and 335 μm mesh nets, and (2) a vertical haul of a PairoVET frame, fitted with 153 μm mesh from a maximum depth of 70 m. Flow-through instruments are used to sample near-surface T, S, fluo-

rescence, and turbidity continuously along the ship's track. Since November 2007, all operations have been conducted at night.

Regional Analyses—Central California

CTD sections extending offshore from Monterey Bay to a distance of 315 km (CalCOFI Line 67) have been carried out quarterly since 1997. CTD station spacing is 10 nm and the water column is sampled to a depth of 1000 m.

Regional Analyses—CalCOFI

Results are presented as contour maps of properties, and as time series of cruise averages over all 66 stations or as anomalies with respect to the 1984–2007 time series. The mixed-layer (ML) depth is calculated using a density criterion and set either to 12 m or to the halfway point between the two sampling depths where the sigma-theta gradient first reaches values larger than 0.002/m, whichever is larger. The 12 m cutoff avoids including the diurnal thermocline in the analysis. This procedure will introduce a positive bias in calculation of the ML depth but, because the bias is consistent, it will not affect the interpretation of patterns. The nitracline depth is defined as the depth where concentrations of nitrate reach values of 1 μM, calculated from measurements at discrete depths using linear interpolation. Mesozooplankton displacement volumes for individual stations were log-transformed and then averaged over all stations.

Regional Analyses—IMECOCAL

The IMECOCAL monitoring program began in autumn 1997, consisting of quarterly cruises surveying 93 stations off Baja California, México (fig. 1). The core oceanographic data set collected at each station includes a CTD/Rosette cast to 1000 m depth, with sensors for pressure, temperature, salinity, dissolved oxygen, and fluorescence. Water samples from the upper 200 m are collected with 5 L Niskin bottles at 0, 10, 20, 50, 100, 150, and 200 m depths to determine dissolved oxygen, chlorophyll *a*, nutrients (NO_3, NO_2, PO_4, SiO_3), and primary production. IMECOCAL cruises schedules, data collection, methods, and analysis are fully described at http://imecocal.cicese.mx.

Remote Sensing

We used satellite-detected monthly mean composite of chlorophyll *a* concentration as a proxy for phytoplankton concentration. While ocean color measurements of chlorophyll *a* in coastal waters are affected by interference from other optically active substances, such as detrital material, dissolved organic substances, and suspended sediments, and some blooms are missed by satellite sensors due to cloud cover, the monthly mean composite of chlorophyll *a* is a robust index of water quality and corresponds to the combined effects of chlorophyll *a* and other optically active substances. We use our archive of full resolution chlorophyll *a* data merged from all available ocean color sensors (http://spg.ucsd.edu/Satellite_Projects/Full_res_sat_time_series_California/Full_res_sat_time_series_California.htm) to find the annual maximum monthly chlorophyll *a* for each pixel. We interpret the time series of the annual maxima as a change in bloom magnitude. We then used the Sen slope estimator to detect trends and their significance in bloom magnitude.

Fish Egg Surveys off California

The planned 2007 survey consisted of three legs: Leg 1, the regular CalCOFI survey, and Legs 2 and 3, the daily egg production method (DEPM) survey. Leg 1 (27 March–12 April) was to occupy six CalCOFI lines (93.3–76.7). Leg 2 (13–20 April) was to occupy six lines northward from line 91.7 out to station 70. Leg 3 (20 April–1 May) was to occupy four CalCOFI lines (73.3–63.3) off central California. Due to equipment problems and weather conditions, Leg 1 ended on 19 April with five CalCOFI lines from 93.3 to 80.0 occupied. Leg 2 from 19–23 April covered three lines from line 91.7 out to station 70 and ended at Port San Luis. Leg 3, from 23 April–1 May, occupied three lines: 76.7, 66.7, and 63.3 due to weather conditions. Thus, the RV *David Starr Jordan* cruise (27 March–1 May) occupied 11 lines (93.3–63.3) out of 17 planned lines; lines were 37 or 74 km apart (fig. 1). Bongo samples were taken at all CalCOFI stations except line 63.3. During Leg 1, CalVET tows were taken only at regular CalCOFI survey stations. During Legs 2 and 3, CalVET tows were taken at 7.4 km intervals on each line after the egg density from each of two consecutive CUFES samples exceeded 1 egg/min and CalVET tows were stopped after the egg density from each of two consecutive continuous underway fish egg sampler (CUFES) samples was less than 1 egg/min (Lo et al. 2005).

Ichthyoplankton and Oceanography

We related hydrographic features observed in data collected on the spring 2007 CalCOFI cruise to the spatial pattern in larval fish and squid. We described the spatial pattern of larval Pacific sardine, northern anchovy, and squid (*Loligo opalescens*), and small zooplankton displacement volume in terms of the spring 2007 anomaly from the median value at each station sampled during March through May from 1985 to 2007. We used the median anomaly because the distribution of larvae is highly right-skewed. Larval distributions were contoured using kriging with covariance parameters for the vari-

ance and range determined by fitting semi-variogram models to the spring 2007 anomalies. Although there was considerable anisotropy in the variograms, we used the values from the omnidirectional models because the along-transect direction contained the most data and dominated the omnidirectional model. Sardine variograms were fit by an exponential model, the zooplankton were fit to a linear model, but both the anchovy and squid presented non-classical patterns due to their extreme patchiness.

Avifauna

Systematic surveys of the distribution and abundance of marine birds have been made on CalCOFI cruises since spring of 1987 (Hyrenbach and Veit 2003). Personnel from the Point Reyes Bird Observatory–Conservation Science (PRBO) conducted at-sea surveys during 2006. Additionally, PRBO has monitored the reproductive performance and diet of seabird populations breeding at the Farallon Islands (37°N, 123°W) since the early 1970s (Sydeman et al. 2001).

To investigate the responses of planktivorous auklets to inter-annual oceanographic variability in the CCS, we related local colony-based (reproductive success) and at-sea (summer abundance) responses to five monthly environmental data sets indicative of oceanographic conditions in the eastern north Pacific Ocean: large-scale variability associated with the Pacific Decadal Oscillation (PDO) and the El Niño/Southern Oscillation Index (ENSO) indices, and regional indices of coastal upwelling at three reference sites (39°N, 36°N, 33°N), to provide complete spatial coverage of the study area. Because previous studies of the diet and productivity of seabird species breeding at southeast Farallon Island have documented lagged responses to local (e.g., upwelling intensity) and remote (e.g., ENSO variability) oceanographic conditions (Ainley et al. 1993, 1995), we included antecedent environmental conditions as explanatory variables in our analysis. To account for the time lags between changes in basin-wide/regional oceanographic conditions and local seabird responses, we considered three distinct time periods: late winter (January–February); early spring (March–April); and late spring (May–June). We used Systat 11.0 (© 2002 SYSTAT Software Inc.) to examine the relationship between the abundance and productivity of planktivorous auklets and 15 environmental variables using Principal Component analysis (PCA).

LARGE-SCALE PATTERNS

Moderate El Niño conditions in the tropical Pacific Ocean decayed rapidly in early 2007 to generally neutral conditions by early spring. A moderate-to-strong La Niña (NOAA CPC Climate Diagnostics Bulletin) developed during the late summer (fig. 2) and sea surface temperature (SST) anomalies in the tropical Pacific Ocean east of the Date Line exceeded –2°C by fall 2007 (fig. 3B). The NOAA CPC Oceanic NINO Index (ONI) during Dec–Jan–Feb 2008 indicates that the La Niña was the strongest since 2000, while the multivariate ENSO index (MEI) (Wolter and Timlin, 1998) was the lowest Jan-Feb MEI value since 1976 (http://www.cdc.noaa.gov/people/klaus.wolter/MEI/). SST anomalies displayed the typical horseshoe pattern of La Niña through fall/winter 2007, continuing into early 2008 (fig. 3C, D). This pattern included below-normal SSTs in the California Current and Gulf of Alaska, and strong above-normal SSTs north of the Bering Strait.

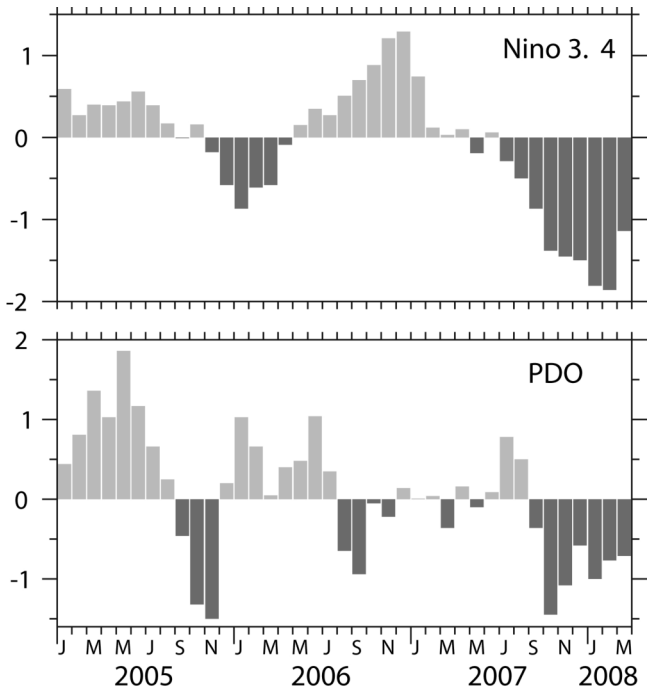

Figure 2. Time series of monthly anomalies of Niño 3.4 (top) and the Pacific Decadal Oscillation index (bottom) for January 2005 to March 2008.

During the same period, the north Pacific Ocean SST anomalies displayed a negative pattern of Pacific Decadal Oscillation (fig. 2) with below-normal SSTs in the California Current and Gulf of Alaska (fig. 3C, D). The positive SST anomalies that have occurred each boreal summer since 2002 north of the Bering Strait reached the highest value of about 2.5°C in 2007. The associated global ocean was much cooler than in 2006, especially in the equatorial Pacific Ocean, northeast Pacific and north Atlantic Ocean, but much warmer in the Arctic. Details on month-to-month and interannual global ocean climate variability can be found at CPC's "Monthly Ocean Briefing" archive (http://www.cpc.ncep.noaa.gov/products/GODAS).

The current La Niña was preconditioned with neg-

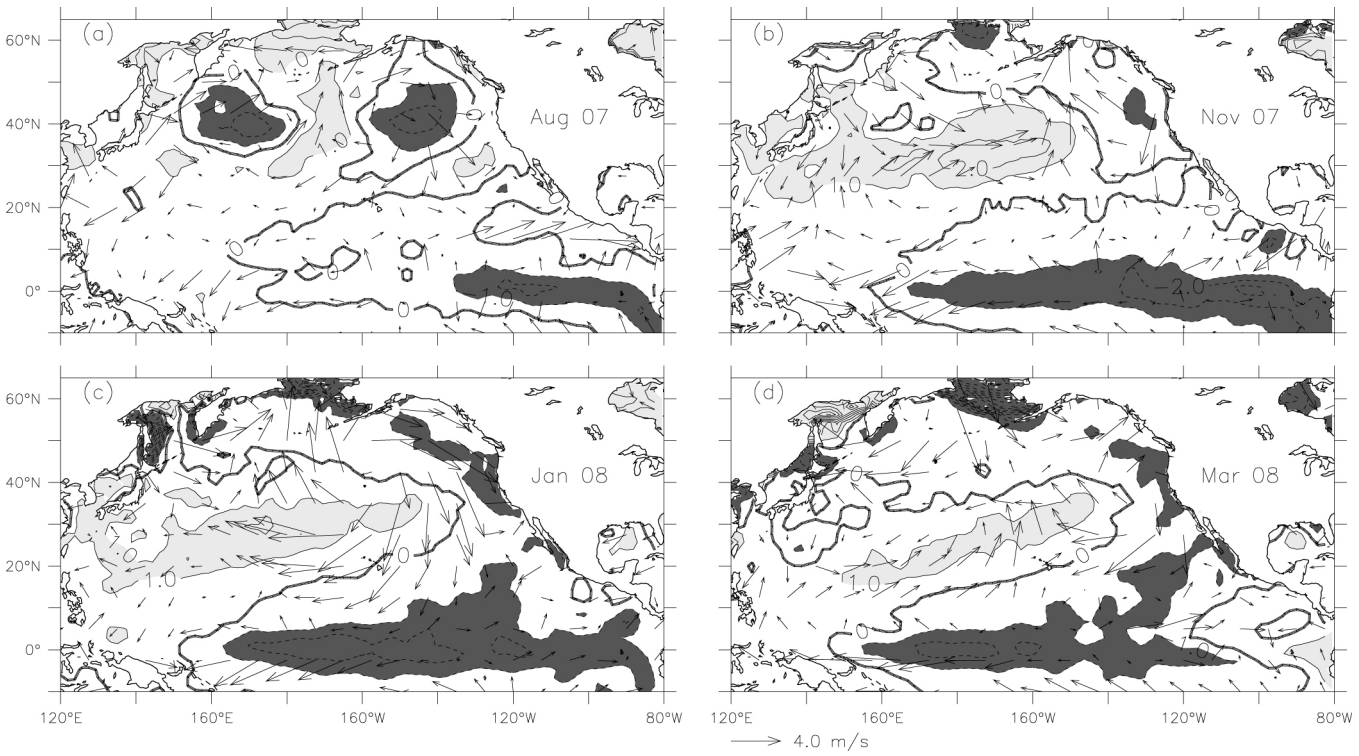

Figure 3. Anomalies of surface wind velocity and sea surface temperature (SST) in the north Pacific Ocean, for (A) August 2007, (B) November 2007, (C) January 2008, and (D) March 2008. Arrows denote magnitude and direction of wind anomaly. Contours denote SST anomaly. Contour interval is 1.0°C. Negative (cool) SST anomalies are shaded. Wind climatology period is 1968–96. SST climatology period is 1950–79. Monthly data obtained from the NOAA-CIRES Climate Diagnostics Center.

ative ocean heat content anomalies in the equatorial eastern Pacific Ocean in spring 2007. When seasonal trade winds intensified in summer 2007, negative subsurface temperature anomalies shoaled to the surface through entrainment at the bottom of the mixed layer, and were then advected westward. Negative SST anomalies first appeared in the far eastern equatorial Pacific and were then displaced westward. La Niña peaked during January–February 2008, and then weakened substantially during March 2008, coincident with a significant reduction of ocean heat content anomalies. The upward trend of the negative SST anomalies near the west coast of South America since mid-December 2007 was related to the westward expansion of westerly wind anomalies in the far eastern Pacific. Recent strengthening of the westerly wind anomalies pushed SSTs off South America to +1°C in March 2008. This westward expansion of negative SST anomalies and development of positive SST anomalies in the eastern Pacific also occurred during the 1999–2000 La Niña.

While the overall circulation in the Pacific in recent months was typical of La Niña, the pattern has been modulated by considerable intraseasonal Madden-Julian Oscillation (MJO) activity, which is characterized by 30–60 day variability in the tropics. Intraseasonal activity was evident in the northeast Pacific throughout much of 2007, with moderate-to-strong MJO activity from November to mid-February 2008 influencing, at times, the region through atmospheric teleconnections. This is illustrated by considerable month-to-month variability on sub-ocean basin scales (fig. 3). Month-to-month SST anomaly changes in the north Pacific have been controlled locally by a combination of surface air-sea heat fluxes and Ekman transport and pumping (open ocean upwelling).

MJO-related winds can significantly affect surface and subsurface conditions across the tropical Pacific. Strong easterly wind anomalies associated with the mid-December 2006 MJO episode led to an oceanic upwelling Kelvin wave that reduced positive ocean heat content anomalies and contributed significantly to the demise of the 2006 El Niño. In early summer 2007, MJO-related westerly wind bursts in the western tropical Pacific reduced negative heat content anomalies. Moderate-to-strong MJO activity from November to mid-February 2008 forced a series of Kelvin waves. The downwelling Kelvin wave episode initiated in January 2008 led to a propagation of positive heat content anomalies across the tropical Pacific, and contributed to a sudden weakening of the La Niña in March 2008. The MJO role in the concurrent warming near the west coast of South America is the subject of further analysis.

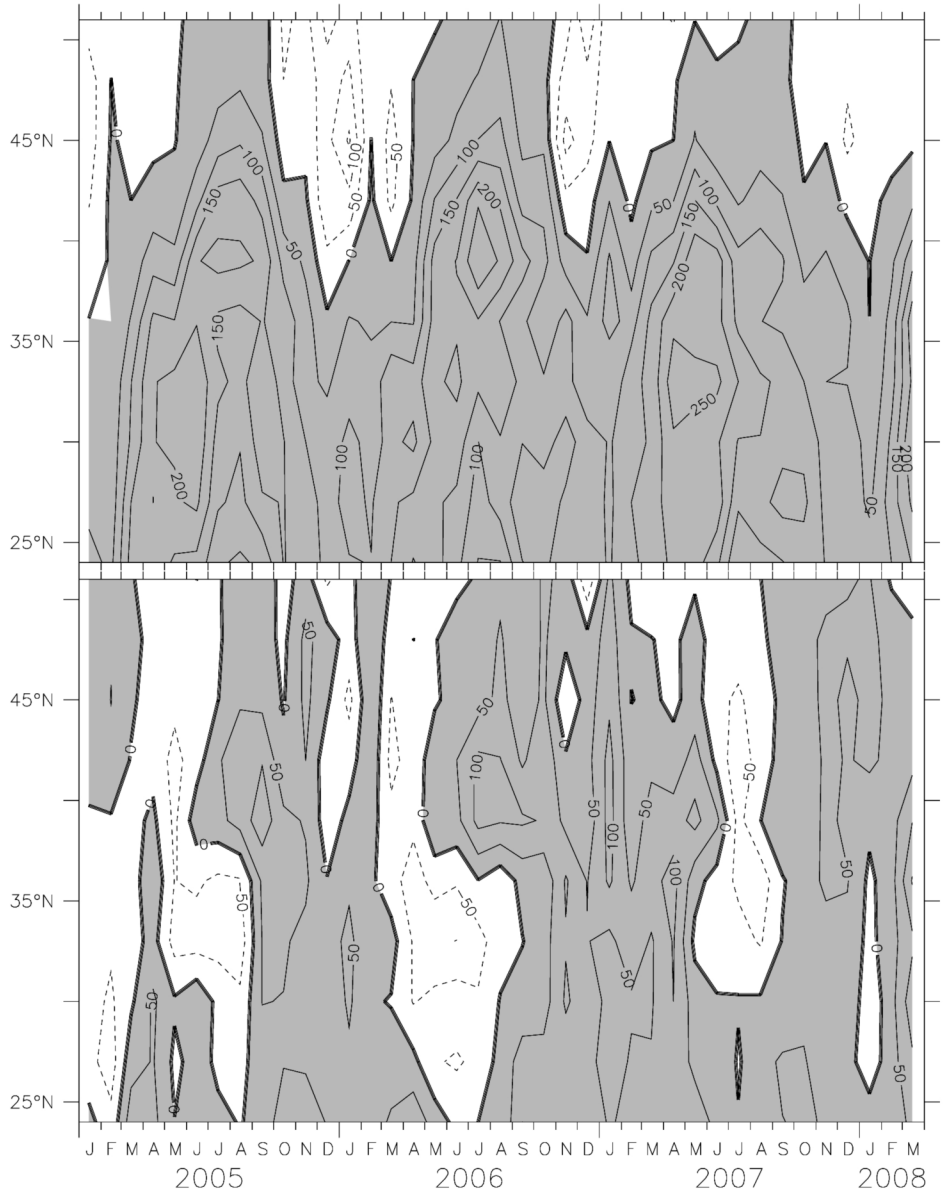

Figure 4. Monthly coastal upwelling index (top) and coastal upwelling index anomaly (bottom) for January 2005–March 2008. Shaded areas denote positive (upwelling-favorable) values in upper panel, and positive anomalies (generally greater than normal upwelling) in lower panel. Anomalies are relative to 1948–67 monthly means. Units are in m^3/s per 100 km of coastline.

The effect of this large-scale pattern on the California Current has been anomalously strong southward coastal winds and stronger than normal coastal upwelling along the West Coast (fig. 4) for most of the year. Strong anticyclonic (clockwise) wind anomalies near the western coast of North America favored coastal upwelling and reduced SST. With the exception of a brief period of negative anomaly (weaker than normal upwelling) in summer 2007, West Coast upwelling index anomalies have been positive since late summer 2006. Wind anomaly patterns in early 2008 reflect anomalously strong high pressure over the northeast Pacific (fig. 3C, D) and very high upwelling (fig. 4). The frequency of relaxation events was higher in summer 2007, roughly 2–4 weeks compared to monthly in most years (fig. 6). This may have influenced recruitment of nearshore species (cf. Farrell et al. 1991). These unusual regional conditions since summer 2007 have occurred during a period of tropical La Niña and negative PDO (fig. 2), both of which are typically associated with an unseasonably cool California Current.

The delayed onset of seasonal upwelling in spring 2005 (fig. 5) and 2006 (Schwing et al. 2006) has been blamed for poor ocean conditions and biological pro-

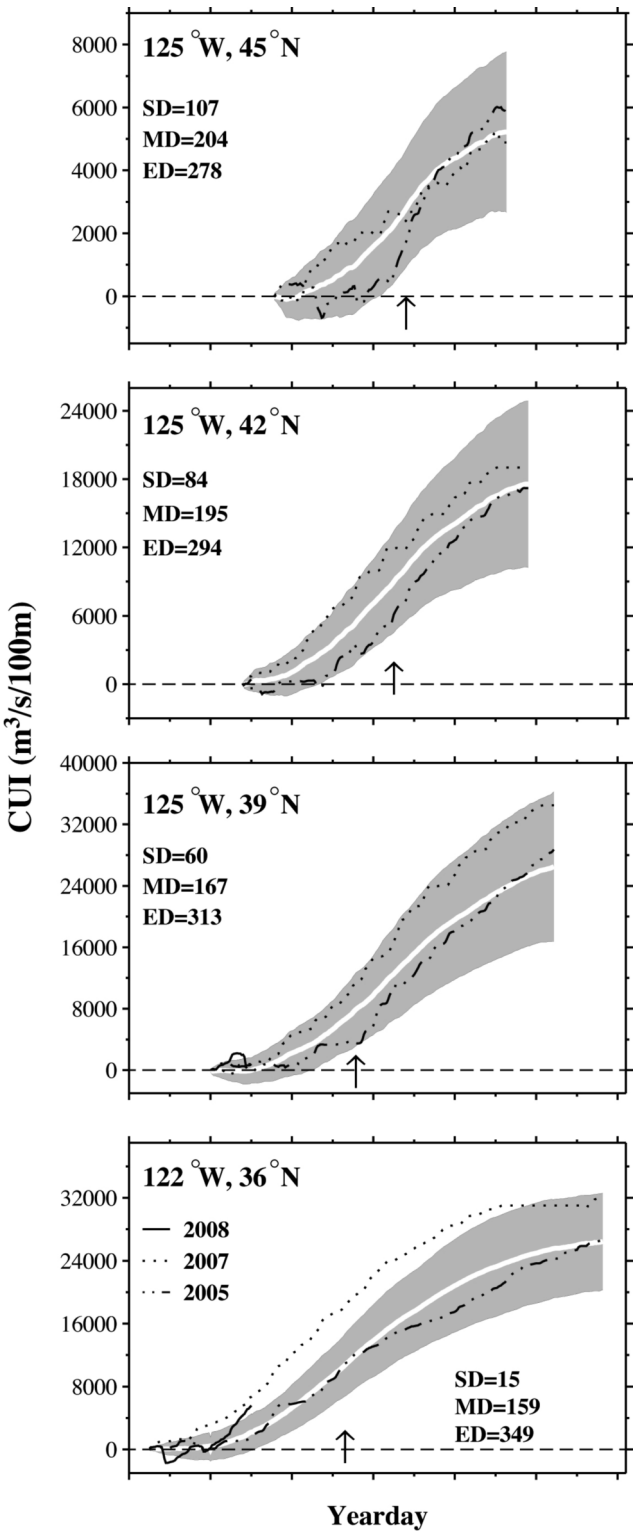

Figure 5. Cumulative upwelling index (CUI; $m^3\ s^{-1}\ 100\ km^{-1}$) for four locations in the California Current. Integration was performed over the climatological upwelling season at each latitude, and arrows mark the time of maximum climatological upwelling at each latitude. Julian days of start (SD) and end (ED) of upwelling season and maximum upwelling are shown for each location. Mean and standard deviation (black solid and shaded areas, respectively), and 2005, 2007, and 2008 are shown.

ductivity and recruitment failures in several populations. Extremely poor returns of Chinook salmon stocks in California, which has triggered the closure of much of the West Coast salmon fishery, are attributed to this. In contrast, the 2007 upwelling season began early, and upwelling remained unseasonably strong through May (fig. 5). Although upwelling reduced substantially in June and July, the cumulative upwelling for the 2007 season was greater than normal in the southern portion of the California Current system. Strong upwelling to date in 2008 indicates an early transition to upwelling this year as well. An important implication of this could be greater ecosystem productivity and reproductive success for many populations.

Conditions at coastal NDBC buoys have reflected these large-scale patterns. Buoy winds have been generally upwelling-favorable (southward), with a number of very strong upwelling episodes (fig. 6). The first half of 2007 was unusual in its relative lack of relaxation events, periods of northward (downwelling) wind when onshore recruitment can occur. Associated buoy SSTs were anomalously cool. The latter half of 2007 featured a strong regular cycle of upwelling/downwelling. The extension of this pattern in the California Current in late-2007 was linked to the active period of tropical MJO. Buoy SSTs have been unseasonably cool since fall 2007.

Remote Sensing

Data from ocean color satellites show that the magnitude of phytoplankton blooms in coastal areas of the California Current increased during the last 11 years (1997–2007, fig. 7). Ocean color data of 1997–2007 showed increased phytoplankton bloom magnitude along most of the West Coast of North America; the increase was weakest in the southern Baja California region (fig. 7). A very similar increase in bloom magnitude has been detected in other eastern boundary upwelling systems (Kahru and Mitchell, 2008). The distribution of the trend in the Gulf of California showed that increased bloom magnitude was characteristic of the eastern boundary region and not of the western boundary region.

Increased blooms in eastern boundary areas may be caused by increased upwelling due to stronger northwesterly winds, but we are unaware of any direct evidence supporting that. The increased blooms off Oregon are likely the cause of the increased "dead zones" of oxygen-depleted water (Service 2004, 2007). It is obvious that some of the observed trend in bloom magnitude is attributable to the strong El Niño of 1997–98 in the start of the time series as suppressed chlorophyll *a* levels in coastal areas of the California Current were associated with the 1997–98 El Niño (Kahru and Mitchell 2000, 2002). However, bloom magnitudes have increased in many areas even after 1997–98. The only larger area

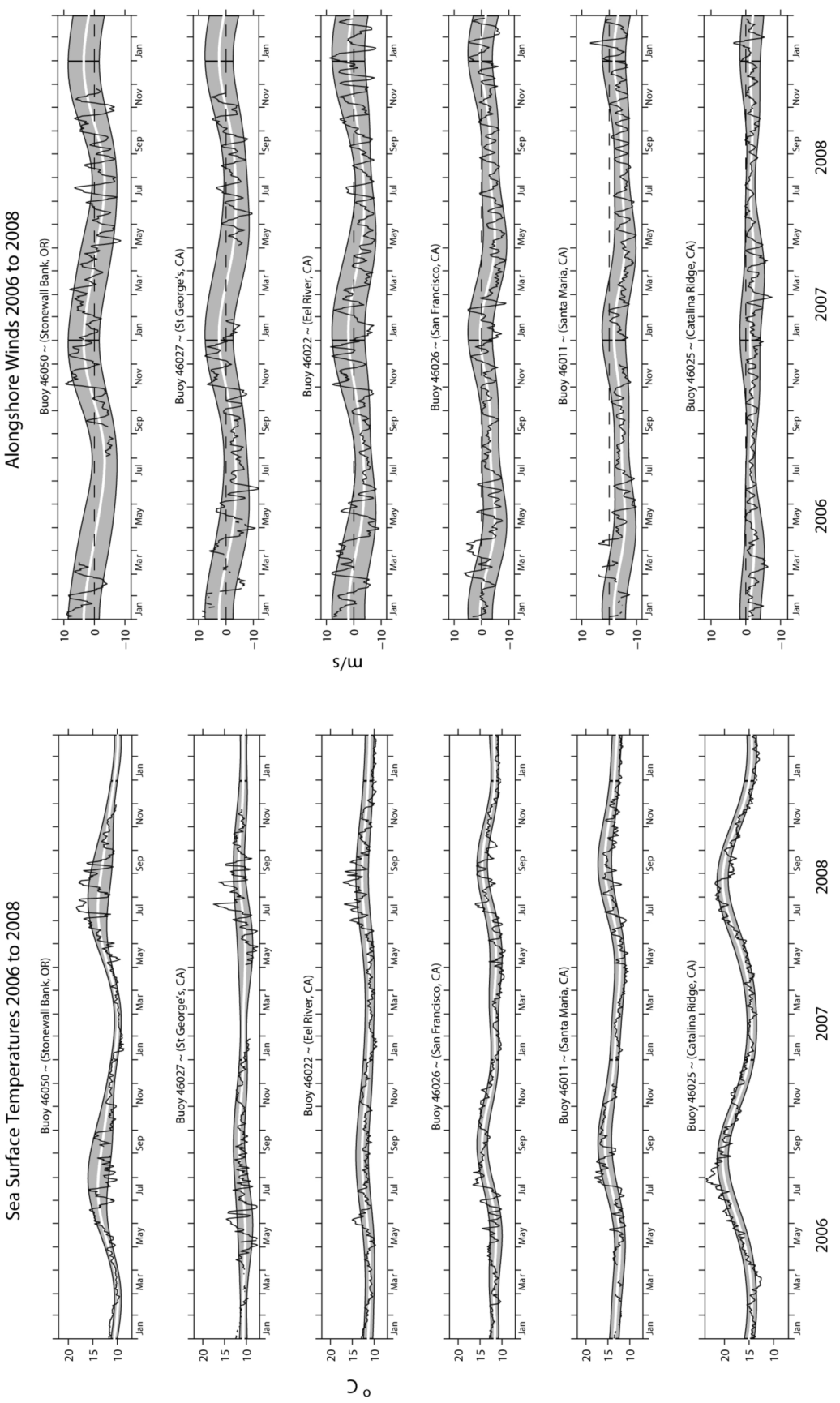

Figure 6. Time series of daily-averaged SST (left) and alongshore winds (right) for January 2006–February 2008 at selected NOAA National Data Buoy Center (NDBC) coastal buoys. Bold lines are the biharmonic annual climatological cycle at each buoy. Shaded areas are the standard errors for each Julian day. Series have been smoothed with a seven-day running mean. Data provided by NOAA NDBC.

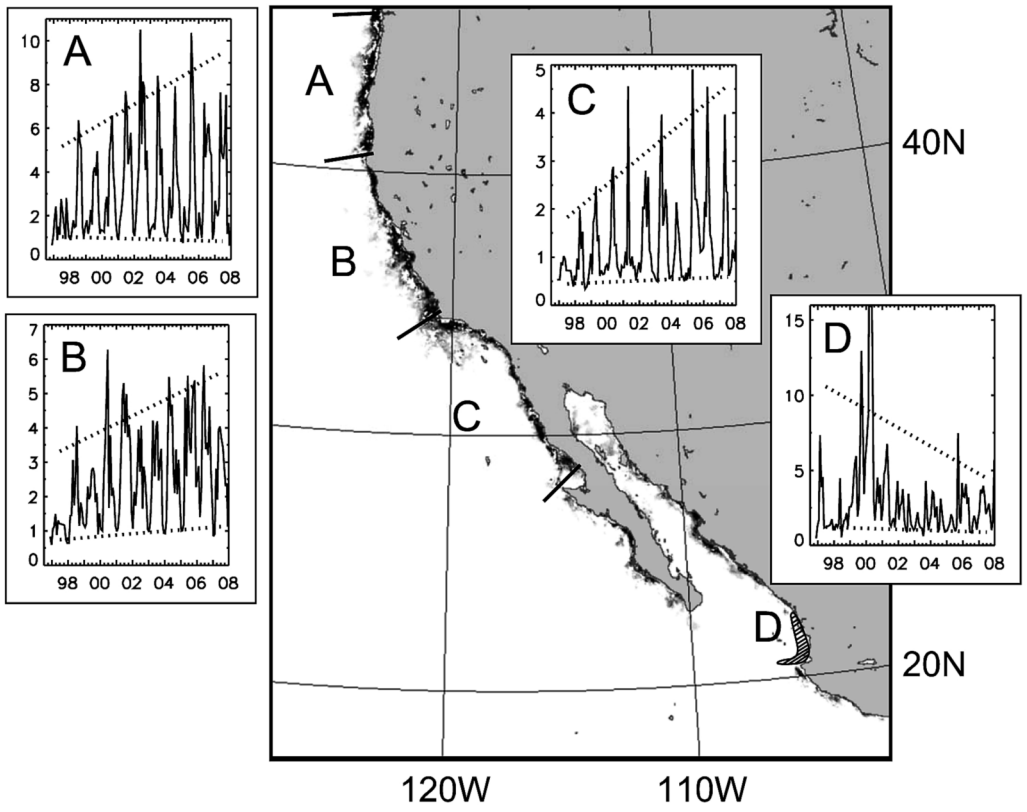

Figure 7. Trends in phytoplankton bloom magnitude detected by ocean color in 1997–2007. Areas of increased bloom magnitude (dark gray) are detected along coasts and no trend (white) is evident in offshore areas. An area of decreased bloom magnitude (striped) is off Mexican states of Nayarit and Jalisco (D). The trend and its significance are estimated using the Sen slope test at 95% confidence level. Individual time series of spatially averaged Chlorophyll *a* (mg/m^3) are shown as insets for 50 km near shore bands off the coast (A, B, C) or in the specified area (D). Linear trends in annual maxima (bloom magnitude) and minima are shown with dotted lines. The trends in maxima are significant at 95% level but the trends in minima are not.

of decreased bloom magnitude was found off the coast of the Mexican states Nayarit and Jalisco and was related to the exceptionally strong harmful algal blooms in that area in 2000.

REGIONAL STUDIES—HYDROGRAPHY

Oregon

SST at the NOAA Weather Buoy 46050 off Newport was slightly below average for most of 2007 with the notable exception of the months of July and August when SST anomalies of + 2.8° and 1.5°C were observed (fig. 6). SST values at our baseline station NH-05 (five miles off Newport, not shown) were also above long-term averages during the summer of 2007, reflecting weak upwelling conditions during July and August (fig. 4). Measurements of temperature and salinity measured every two weeks at a depth of 50 m at one of our baseline stations (NH 05, five miles off Newport) showed that the deep waters in spring and summer of 2007 were very cold and relatively salty (not shown). In fact, salinities were the highest that we have measured and temperatures were the fourth coldest since we began making CTD measurements off Newport in 1997.

A time series of temperature measured at a depth of 150 m at a shelf break station off Newport (NH 25, station depth of 300 m) shows a strong seasonal cycle as well as interannual variations (fig. 8). The water is warm and relatively fresh during the winter but cold and salty during summer. Temperatures at 150 m depth were cool during summers of 1999–2002 (ranging from 7.39°C in 1999 to 7.24°C in 2002), but warm in summer of 2003–06, (7.56°C in 2003, 7.71°C in 2004, 7.65°C in 2005, and 7.69°C in 2006). Cooler temperatures were again seen in summer 2007 at 7.34°C.

Salinity at 150 m continues to show a trend toward increased salinity in all months, beginning in spring 2005, similar to observations made during most months of the years 1999–2002. From this (albeit limited data set), it appears that relatively warm and fresh water occurs at depth during the positive phase of the PDO and colder and saltier water occurs during the negative phase, supporting a hypothesis that different water types occur off Oregon as a function of the phase of the PDO.

Northern California

Observations were made along the Trinidad Head line (41°3.50'N) from spring 2007 through winter 2008. Upwelling off northern California started early in the spring of 2007 and was unusually strong (fig. 4, fig. 5). Observations during spring 2007 captured a dominant signal of persistent upwelling, modified by a relaxation-downwelling that coincided with sampling (CS0704, fig. 9, top panels). The relaxation event likely contributed to the establishment of a phytoplankton bloom along the coast. By the summer, upwelling had weakened and the upper 50 m of the water column had stratified along the observational line. Offshore, a subsurface chlorophyll *a* maximum had formed with concentrations as high as 8 mg/m^3. Inshore, these high concentrations were observed in the mixed layer, likely due to the effects of nutrients brought into the mixed layer by the persistent, albeit weaker, upwelling in the area (fig. 4). Water-column structure in November 2007 reflected the effects of localized downwelling. In contrast, conditions during the 2007–08 winter and early spring were marked by shoaling of cooler, saltier water towards the coast (fig. 9, lower three rows), consistent with the trends in the monthly upwelling index between 39°N and 42°N (fig. 4).

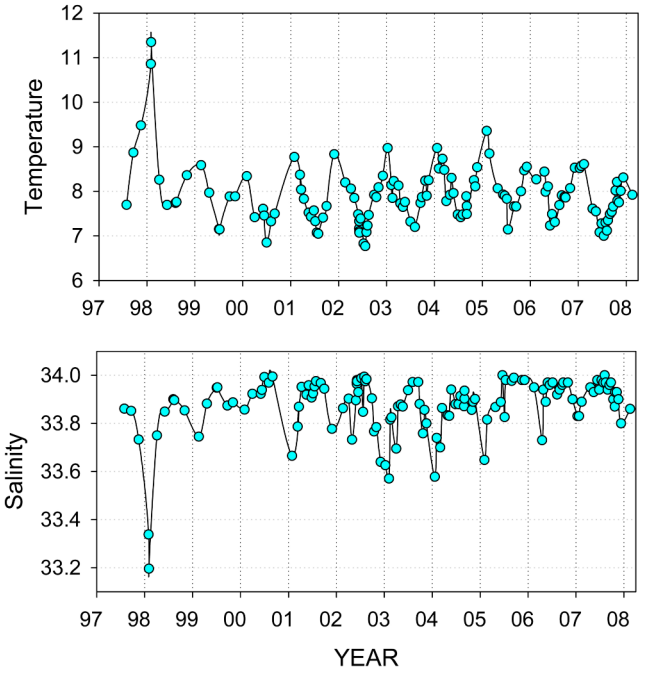

Figure 8. Time series of temperature and salinity measured at a depth of 150 m at station NH 25 (25 miles off Newport); station depth is 297 m.

Central California

Hydrographic data have been collected in the Monterey Bay region from mid-1988 through the end of 2007 and are presented here as anomalies (fig. 10). Temperature and salinity anomalies are inversely correlated and show that spring and summer temperature (salinity) anomalies were 1°C (ΔS = 0.04 psu) cooler (saltier) than normal, most likely due to the strong and persistent upwelling-favorable winds that occurred. Summer chlorophyll *a* concentrations remained about 3 mg/m^3 higher than normal for the fourth year in a row. This marks the eighth year since 1999 that positive anomalies have occurred. Dinoflagellate concentrations returned to normal in Monterey Bay after three years of higher than normal abundance.

Hydrographic stations along CalCOFI lines 67 (off Monterey) and 60 (off San Francisco) to station 90 were occupied in June and November 2007 (Rago et al. 2007, 2008). Near-surface results of June measurements are shown in Figure 11. Off San Francisco, the core of southward geostrophic flow at the surface was centered at 124W. Along line 67, geostrophic flow was weaker and somewhat farther offshore to the southwest of Monterey, in part due to a cyclonic eddy at the entrance to Monterey Bay. Inshore, 10 m waters were strongly affected by coastal upwelling with temperatures less than 11°C in the Gulf of the Farallones and salinities greater than 33.8 psu in both the Gulf and Monterey Bay. Offshore, the core of subarctic waters (S < 32.8) was observed along the outer half of line 60 (off San Francisco) and followed the 0.96 dynamic meter isostere to the south, where it was narrower and deeper at line 67. At 10 m, warmest waters (15°C) were at the western corner of line 60. Chlorophyll-*a* concentrations at 10 m exceeded 4 mg/m^3 at inshore stations in Monterey Bay and the Gulf of the Farallones, decreasing offshore where they were less than 0.5 mg/m^3.

In November (fig. 12), the California Current flowed to the east through the western portion of the sampling grid, turning to the southeast and exiting at about the middle of line 67. This flow was oriented along the 0.88–0.92 dynamic meter isosteres and was also marked at 10 m by S = 32.8 psu and 14.5°–15°C. Waters in Monterey Bay and the Gulf of the Farallones were colder (<13°C) with higher salinity (~33.3) than those found farther offshore. Chorophyll *a* at 10 m was between 0.09 and 0.27 mg/m^3, except at the head of Monterey Bay (Drakes Bay), where 1.6 (0.9) mg/m^3 was observed.

Compared with the 1988–2001 climatology (Collins et al. 2003), conditions to the southwest of Monterey (Line 67) indicated that subarctic influences (vs. equatorial) were stronger. For example, Figures 11 and 12 show the inshore edge of the California Current (marked by S = 32.9–33.0) intersecting the section at about its halfway point, 150 km from Monterey Bay. During 1988–2003, the inshore edge of the California Current was found near the offshore limit of the section except during the period of the 1997–98 El Niño. Central

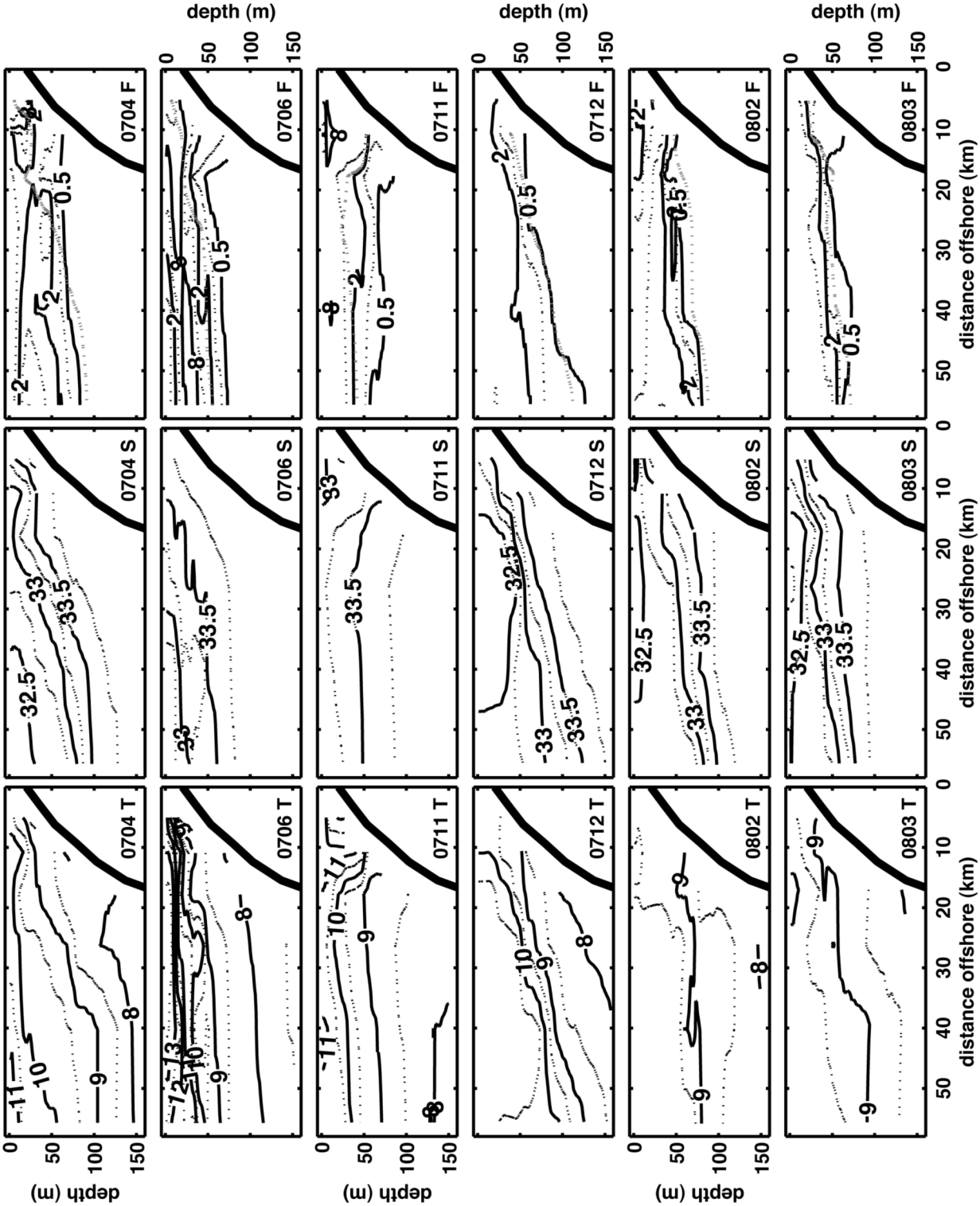

Figure 9. Temperature (left panels), salinity (middle panels), and estimated chlorophyll (converted from fluorescence, right panels) for surveys of the Trinidad Head line from April 2007 to March 2008. Label in lower right of each panel indicates the cruise (YYMM). Temperature and salinity are contoured on a linear scale. Chlorophyll is contoured on a geometric scale; contour line values differ by a factor of two. Grey dotted line on fluorescence plots indicates the σ_t = 25.8 isopycnal. Approximate bottom depth is denoted by the solid dark line in lower right of each panel.

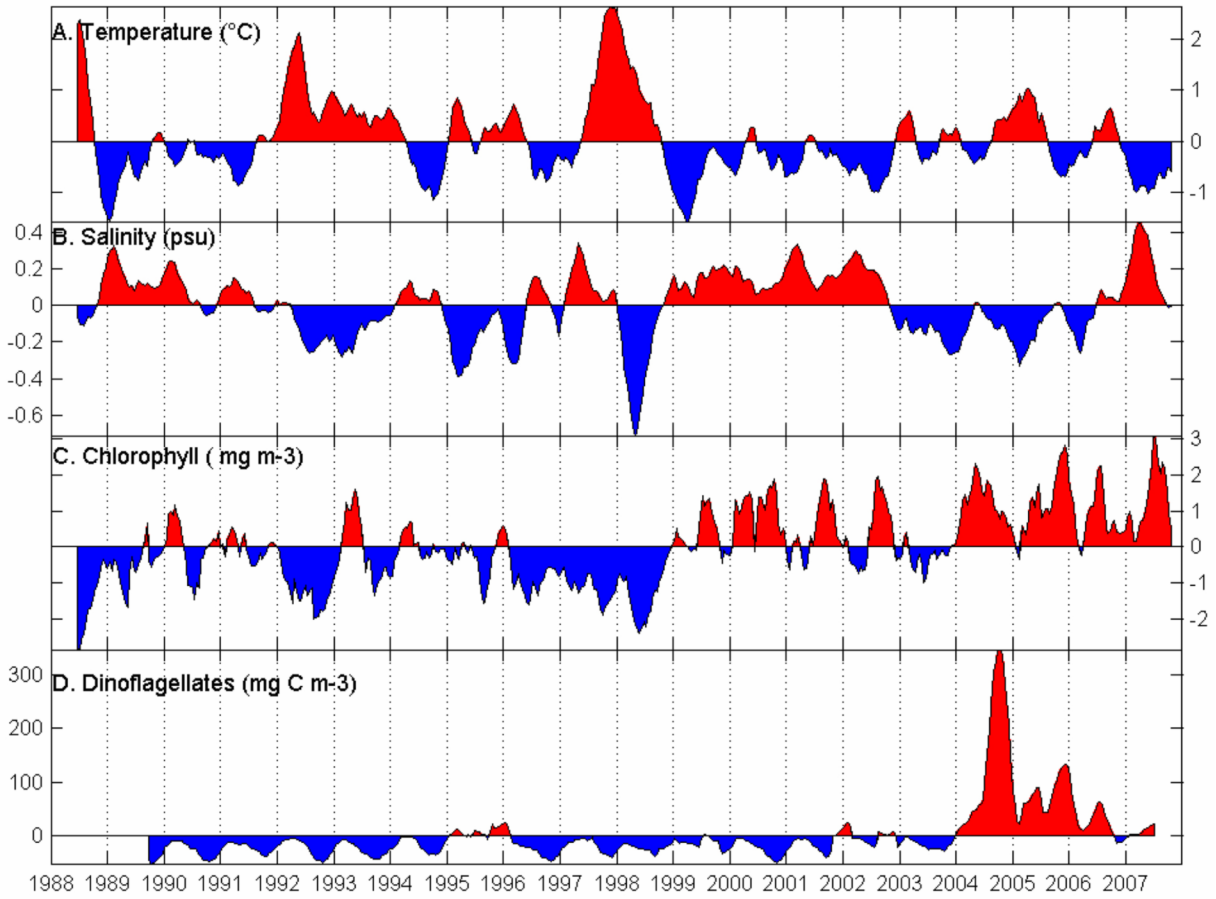

Figure 10. Ocean anomalies for the Monterey Bay region. Data are from Monterey Bay oceanographic stations which have been sampled triweekly since mid-1988.

California conditions reported by Goericke et al. (2007) continued. The mean halocline temperatures remained low, 8.8°C, and the thermocline salinity (34.33) and deep salinity (34.1) continued to freshen. For upper waters (T > 10°C), strong summer upwelling conditions (fig. 5) resulted in a mean salinity of 33.3 in June, which by November had decreased to 33.0.

Southern California: *CalCOFI Cruises*

This year's report on conditions off southern California is based on four cruises in April, July, and November of 2007 and January of 2008 covering 66 stations off southern California (fig. 1). Off southern California, upwelling in the spring of 2007 began slightly early and was slightly stronger than usual (fig. 5). Mixed-layer temperatures, averaged over the 66-station CalCOFI grid, were significantly below long-term averages for the entire time period (fig. 13A), consistent with the basin-wide La Niña conditions described above. With the exception of the summer of 2007, mixed-layer depths were deeper than long-term averages throughout the year (fig. 13B). At the beginning of 2007, mixed-layer salinity was anomalously high, but decreased over the course of the year to values close to the long-term average (fig. 13C). At the beginning of the year temperature at a depth of 200 m was slightly above long-term values (fig. 14A), similar to values observed over the last eight years. By the end of the year and the beginning of 2008 temperatures had dropped below long-term averages. Salinities at 200 m have been decoupled from mixed-layer salinities over the last 8 years; these continued to be significantly higher than long-term averages (fig. 14B). TS (temperature-salinity) plots for different regions of the CalCOFI study area illustrate that sub regions of the study area responded differently to the basin-scale forcing. Salinities in 2007 in the upper thermocline and the mixed layer were significantly higher than long-term averages in the coastal areas and the CC South; in the CC North and at the edge of the central gyres these were close to long-term averages (e.g., fig. 15). In contrast, temperatures in 2007 in the upper thermocline and the mixed layer were lower than long-term averages in the offshore areas (edge of the gyre, CC North and South) but not in the coastal areas (e.g., fig. 15C).

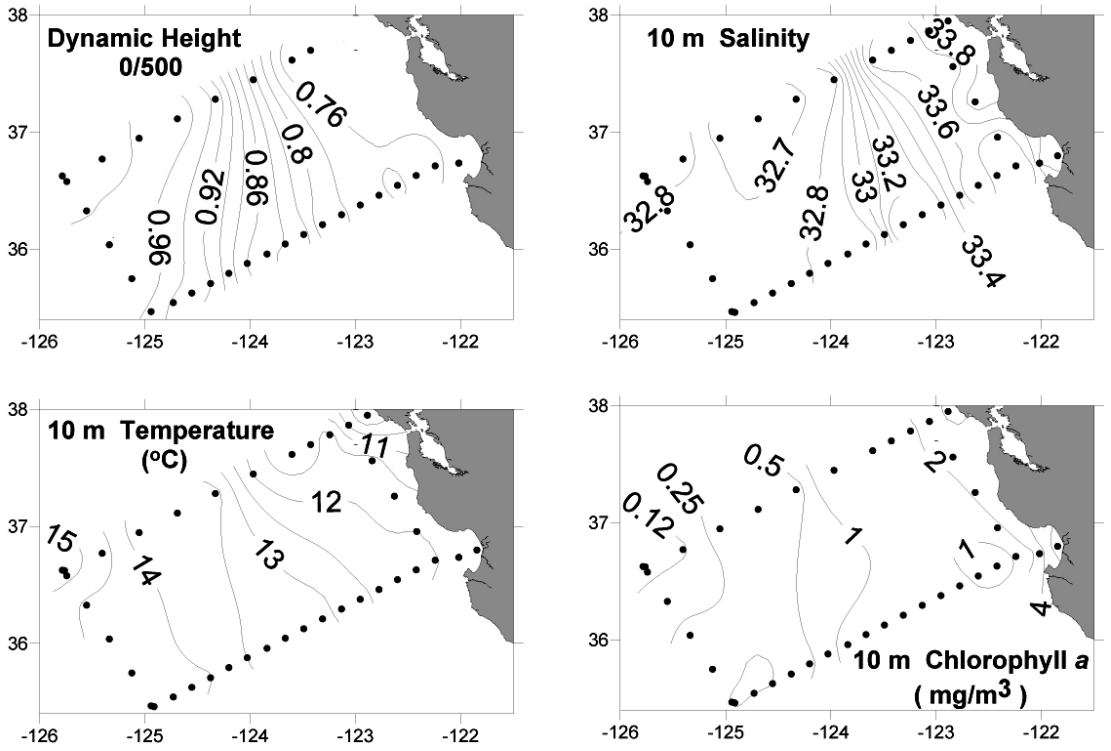

Figure 11. Spatial patterns of hydrographic properties off central California during June 4–9, 2007 (NOAA Ship *McArthur II*). Dynamic height for the surface relative to 500 dbars in dynamic meters (upper left). Salinity at 10 m (upper right). Temperature, °C, at 10 m (lower left). Chlorophyll *a*, mg/m^3, at 10 m (lower right).

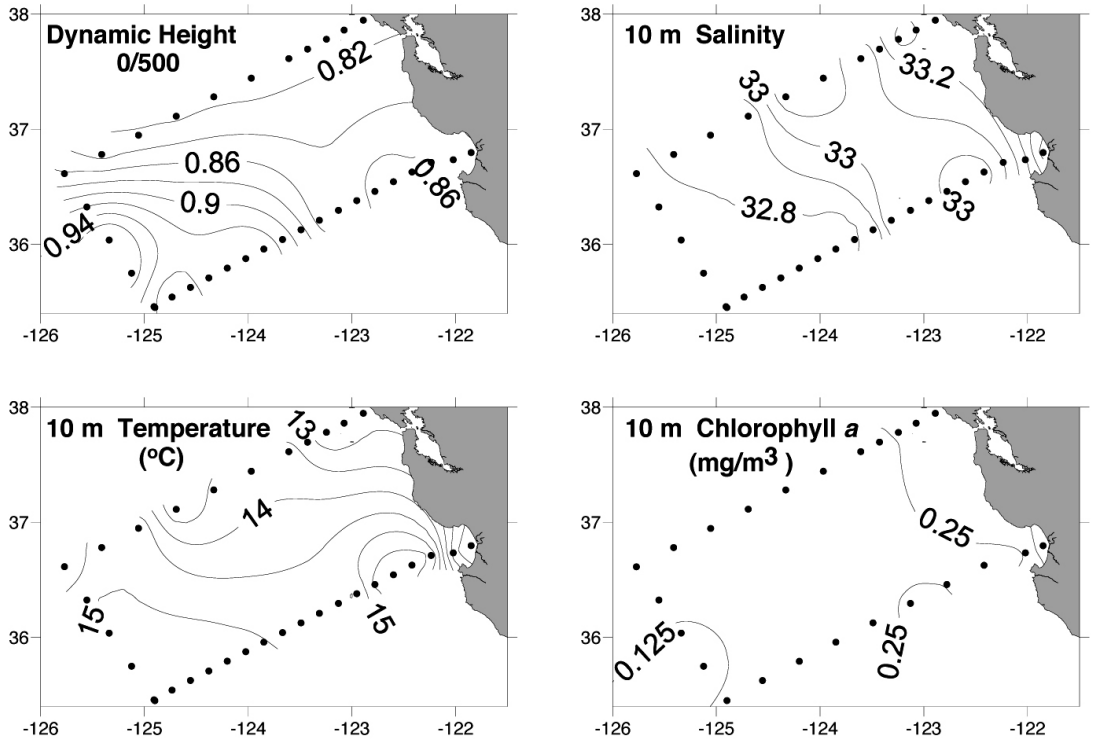

Figure 12. As Figure 11, except during 6–10 November 2007 (NOAA RV *David Starr Jordan*).

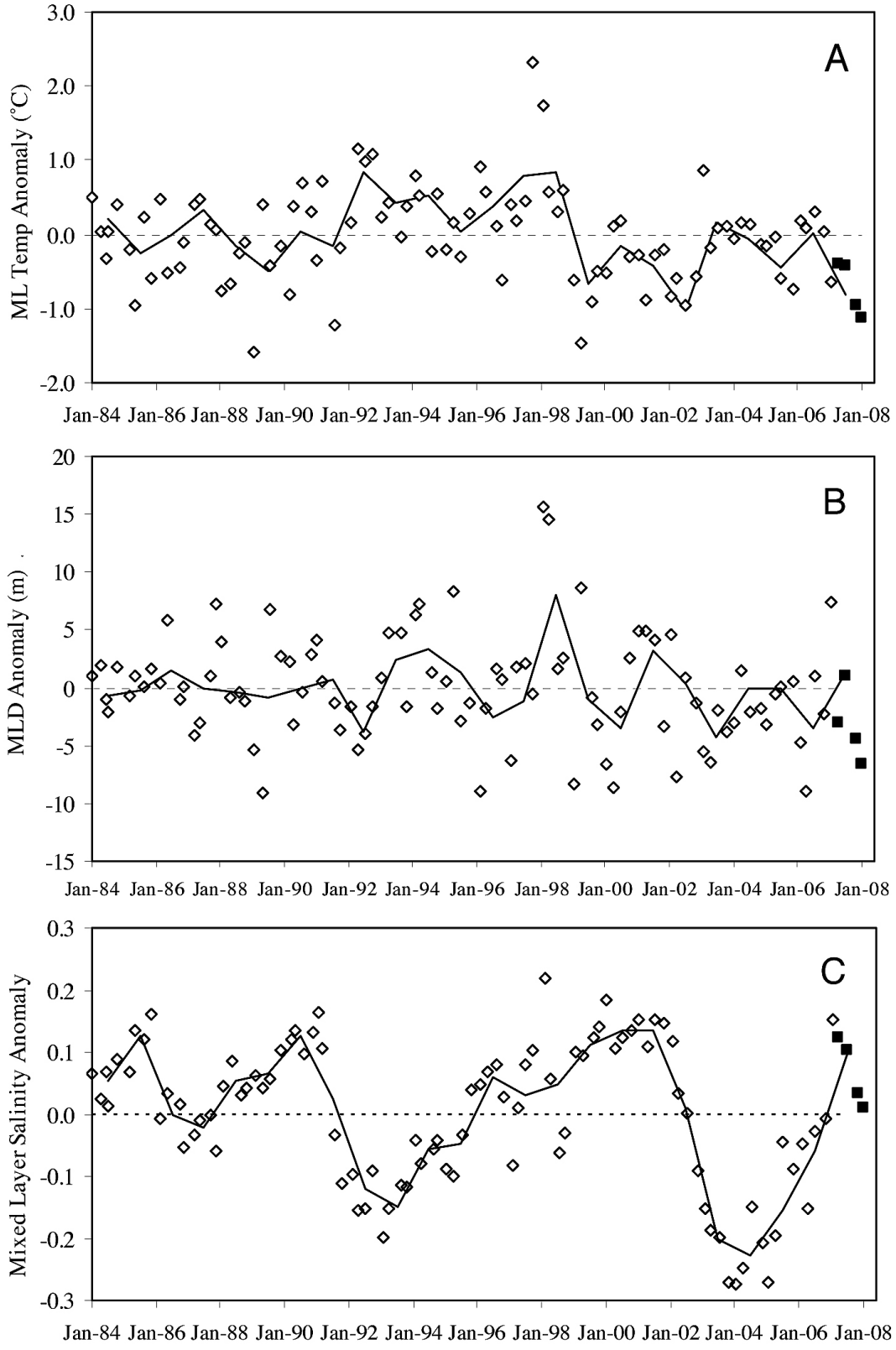

Figure 13. Anomalies of mixed-layer (ML) temperature (A), ML depth (B), and ML salinity (C) off southern California (CalCOFI standard grid, Figure 1). Data from the last four CalCOFI cruises are plotted as solid symbols, data from previous cruises are plotted as open diamonds. The solid lines represent the annual averages and the dotted lines the climatological mean, which in the case of anomalies is zero.

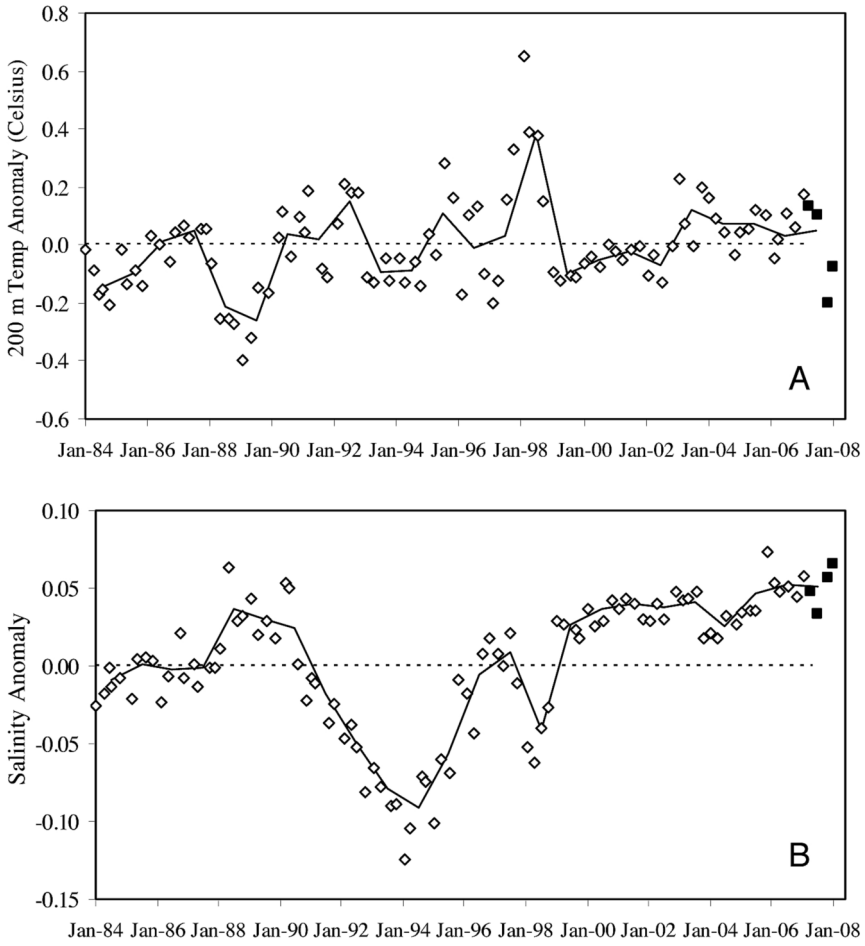

Figure 14. Anomalies of temperature (A) and salinity (B) at a depth of 200 m, calculated and presented as described above for Figure 12.

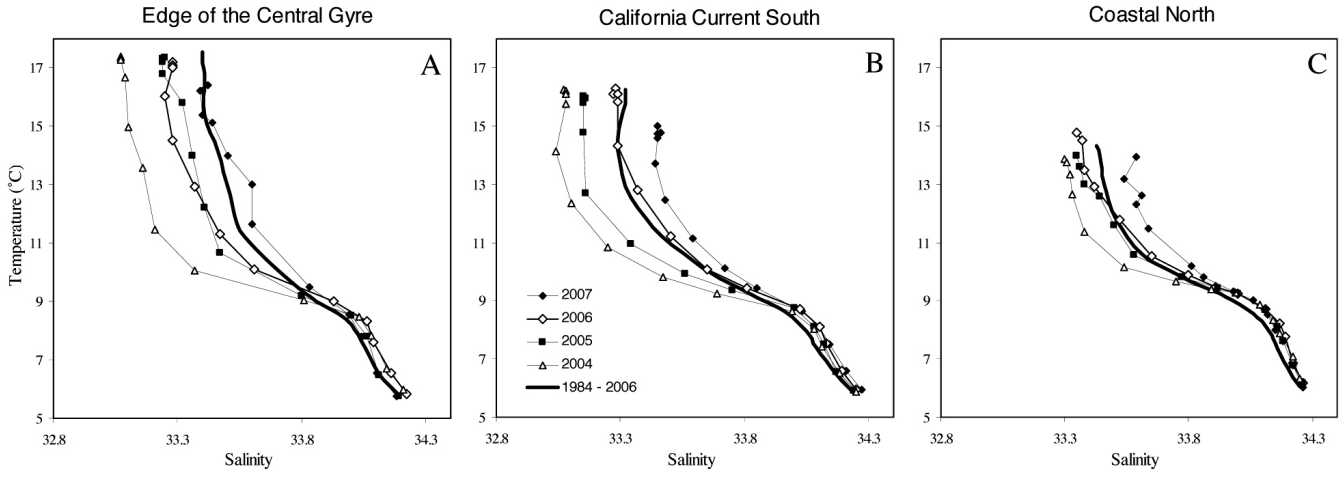

Figure 15. TS plots for three representative areas of the CalCOFI region. A. the edge of the central gyre (Lines 90–93, Stations 100–120), B. the southern California Current region (Lines 87–93, Stations 60–90), and C. the coastal areas in the north (Lines 77–80, Stations 60 and inshore). Each data point represents the average TS characteristic of one standard depth level for the specified time periods, i.e., 1984–2006, 2004, 2005, 2006, and 2007.

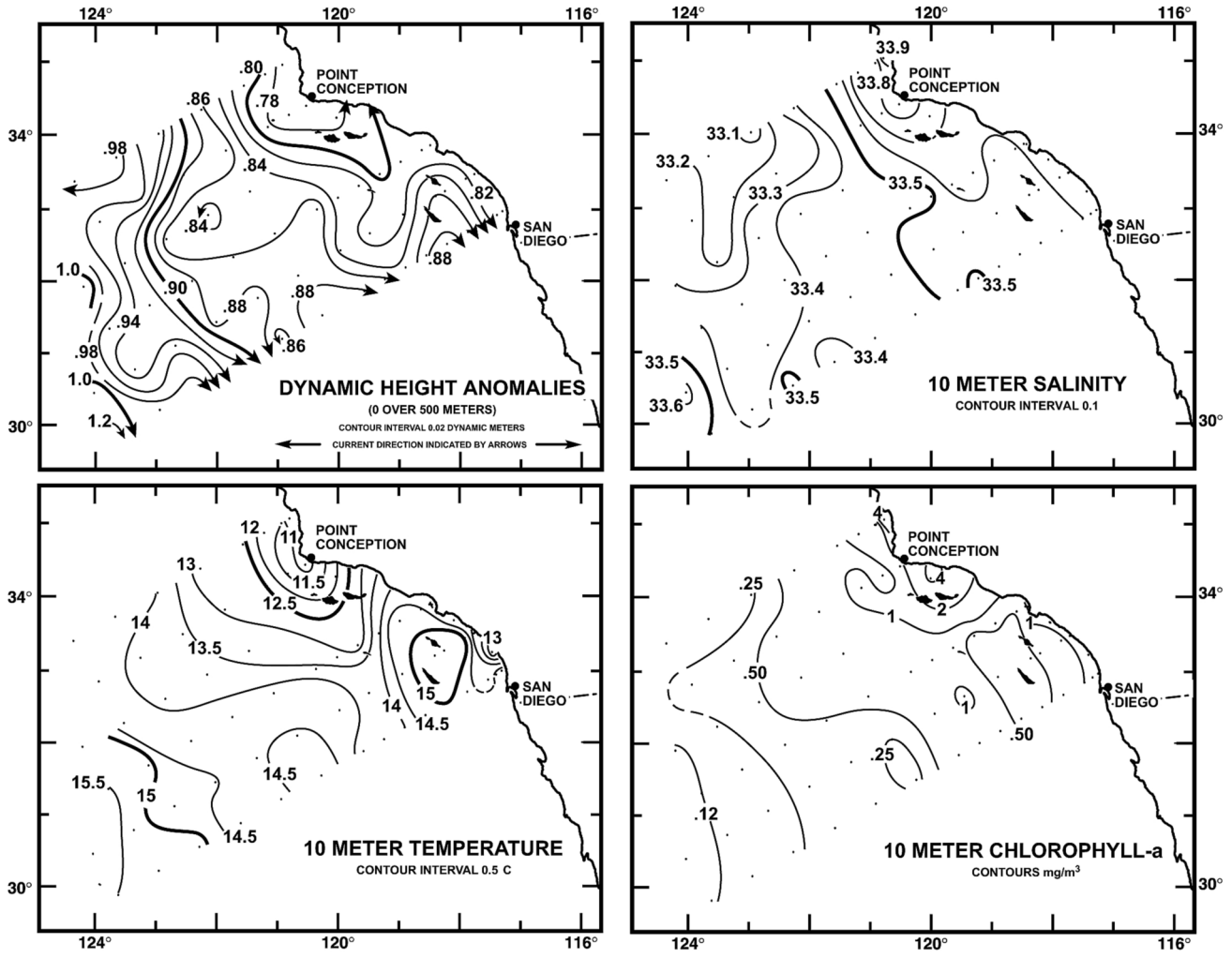

Figure 16. Spatial patterns for CalCOFI cruise 0704 including upper-ocean geostrophic flow estimated from the 0/500 dbar dynamic height field, 10 m salinity, 10 m temperature, and 10 m chlorophyll *a*.

CalCOFI Cruise 0704
(3 March–25 April 2007; fig. 16)

In the spring of 2007 the California Current (CC) entered the CalCOFI study region at the center of line 77, flowed southwest and turned on line 83 southeast to exit the area between stations 93.080 and 93.100. The Southern California Eddy (SCE) had not yet formed. A current loop with anticyclonic flow (downwelling in its center) was found at station 93.40. The northern coastal areas were strongly affected by coastal upwelling, which left its characteristic mark of low temperatures (<12.5 °C) and high salinities (>33.6) in these areas. The center of the study area was characterized by small dynamic height gradients. A small cyclonic eddy was present at station 83.080. Unusually high concentrations of nitrate were observed along lines 77 and 80, out to stations 60 and 70. Unusually high concentrations of nitrate were also observed along line 87, stations 45 to 55. Observations on the inshore portion of line 83 were not carried out due to bad weather. Biologically the system had not yet responded to the enrichment of the euphotic zone with plant nutrients; concentrations of chlorophyll *a* in the northern coastal area, with the exception of the Santa Barbara basin, were low and below long-term averages for the respective stations.

CalCOFI Cruise 0707
(28 June–13 July 2007; fig. 17)

In the summer of 2007 the CC entered the study area still through the center of line 77 but had begun to meander in and out of the study area along its western edge. The cyclonic eddy centered on station 83.080 was still present. A strong poleward flow was observed throughout the study area. The SCE had formed by now, centered on station 87.050. The salinity field followed the flow fields with low salinities associated with the CC

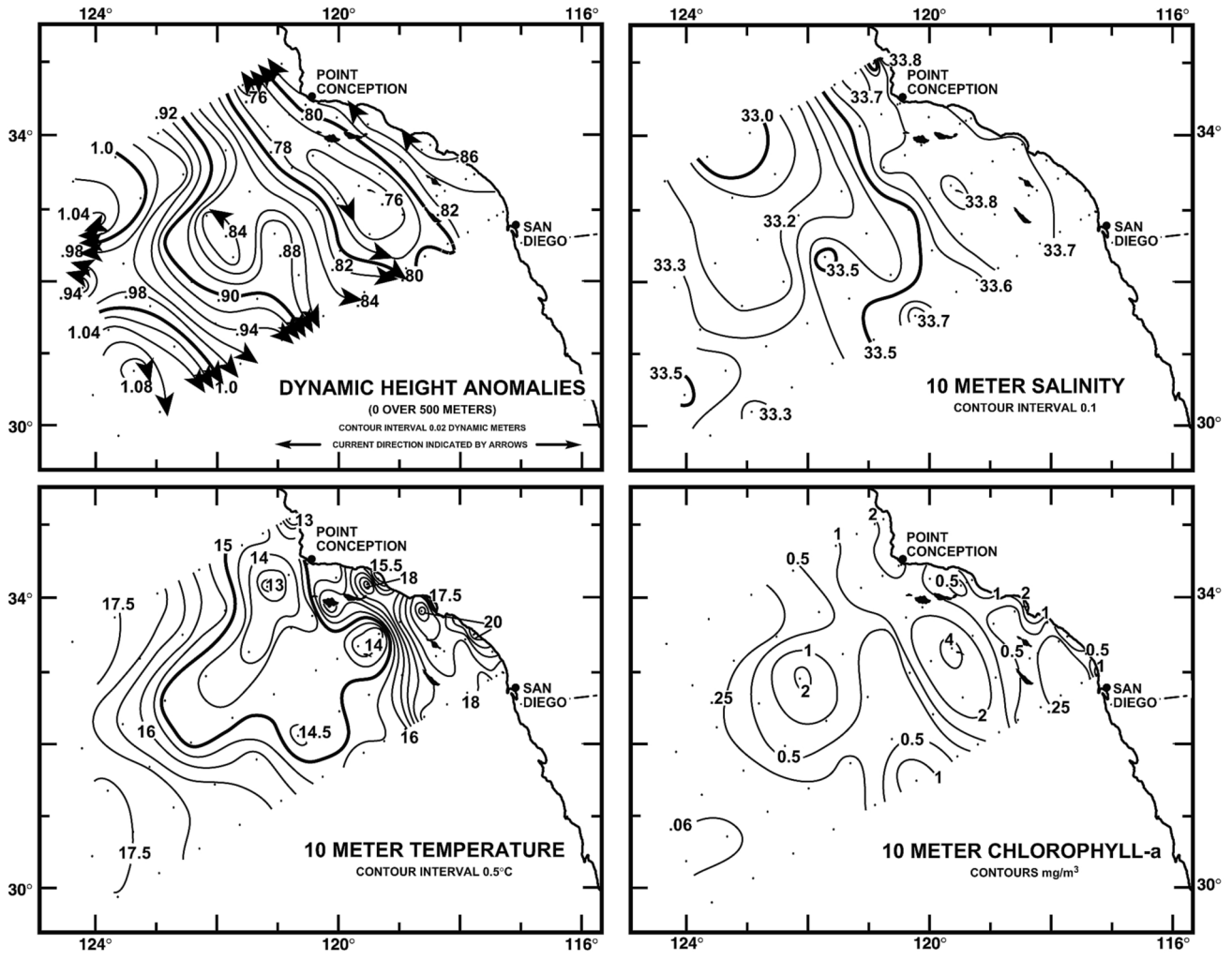

Figure 17. Spatial patterns for CalCOFI cruise 0707 including upper-ocean geostrophic flow estimated from the 0/500 dbar dynamic height field, 10 m salinity, 10 m temperature, and 10 m chlorophyll *a*.

and higher salinities along the coast and the center of the SCE. Unusually high concentrations of nitrate were observed in the region roughly demarcated by the 15°C isotherm, with concentrations in this area up to 10 μM. High concentrations of chlorophyll *a* observed during the summer—along the coast and associated with cyclonic eddies, i.e., the SCE and the eddy at station 83.080—did not coincide with areas of high nitrate concentrations. This suggests that phytoplankton growth may have been limited by nutrients other than nitrate, e.g., iron (King and Barbeau 2007).

CalCOFI Cruise 0711 (2–8 November; fig. 18)

In the fall of 2007 the CC entered the study domain from the northwest and formed a strong loop centered on lines 80 and 83, first flowing northeast and then southwest to the offshore portions of lines 90 and 93. The CC exited the study domain along the offshore portions of line 93. The SCE was still centered on station 87.050. Poleward flow along the coast had weakened. Temperature at 10 m ranged from 15° to 17°C with the exception of a tongue of colder water extending southeast from Point Conception. Concentrations of chlorophyll *a* were low throughout the domain with high concentrations only observed along the coast.

CalCOFI Cruise 0801 (7–25 January 2008; fig. 19)

In January 2008 the CC entered the study area through the center of line 77 and split up into three branches. One branch formed a current loop in the offshore areas of lines 83 to 77 and left the area through the offshore portions of lines 80 and 77. The main branch, marked by the 0.90 dyn. m isostere, flowed southeast, exiting the area along the offshore portion of line 93. It is possible that the CC formed an eddy southwest of the study area, which would explain the strong flow

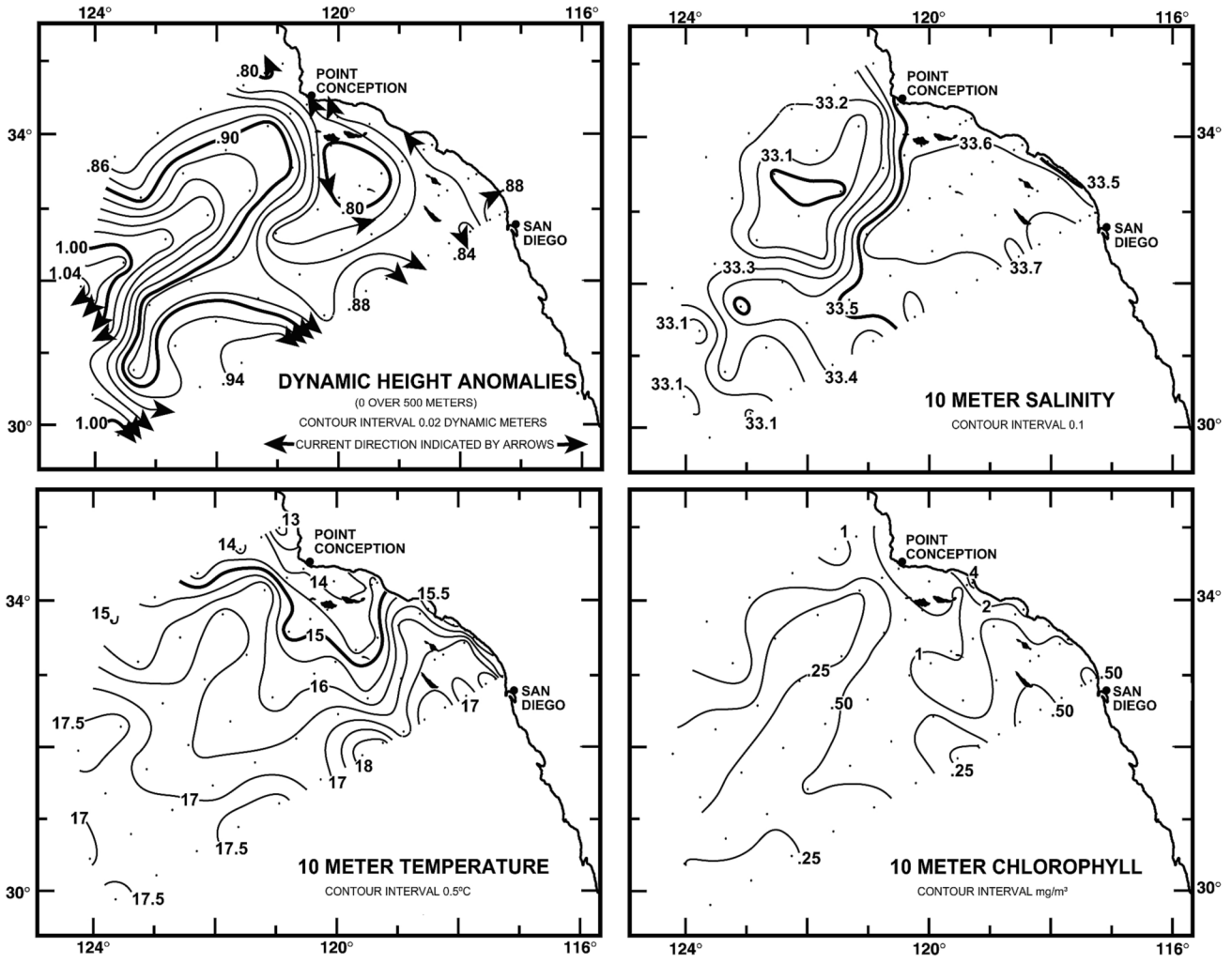

Figure 18. Spatial patterns for CalCOFI cruise 0711 including upper-ocean geostrophic flow estimated from the 0/500 dbar dynamic height field, 10 m salinity, 10 m temperature, and 10 m chlorophyll *a*. Data used for these plots are still preliminary.

coming from the termini of lines 90 and 93, to merge with the CC in the vicinity of stations 93.100 to 93.090. Low salinities of 32.9 along line 77 mark the core of the CC. Relatively low salinities off and south of Point Conception show that upwelling has not yet set in. Temperatures at 10 m were low over large areas of the region. Temperatures of less than 13°C in the northern area of the study area and less than 14°C in the southern area coincided with elevated concentrations of nitrate in the mixed layer. Concentrations of chlorophyll *a* were uniformly low over most of the area with the exception of some coastal regions.

Baja California: *IMECOCAL Cruises*

IMECOCAL surveys off Baja California were conducted in the spring and summer of 2007 and the winter of 2008. In contrast to other areas described above, lower temperatures were not observed off Baja California during the study period, in spite of basin-wide La Niña conditions. Temperatures above the pycnocline in the northern section of the study area were close to long-term averages in 2007; in the southern section these temperatures were actually above long-term averages (fig. 20). Similar to observations to the north, salinity above the pycnocline was significantly higher in both areas during 2007, particularly the southern area (fig. 20). By January 2008, 10 m salinity anomalies were slightly negative (data not shown), similar to observation in the CalCOFI study area to the north. During the January to February 2008 survey (fig. 23) out-of-season upwelling was observed off Ensenada and farther south.

IMECOCAL 0704 (26 April–7 May 2007; fig. 21)

Due to bad weather, it was only possible to cover stations north of line 120. The California Current was found approximately 100 km offshore, splitting in two

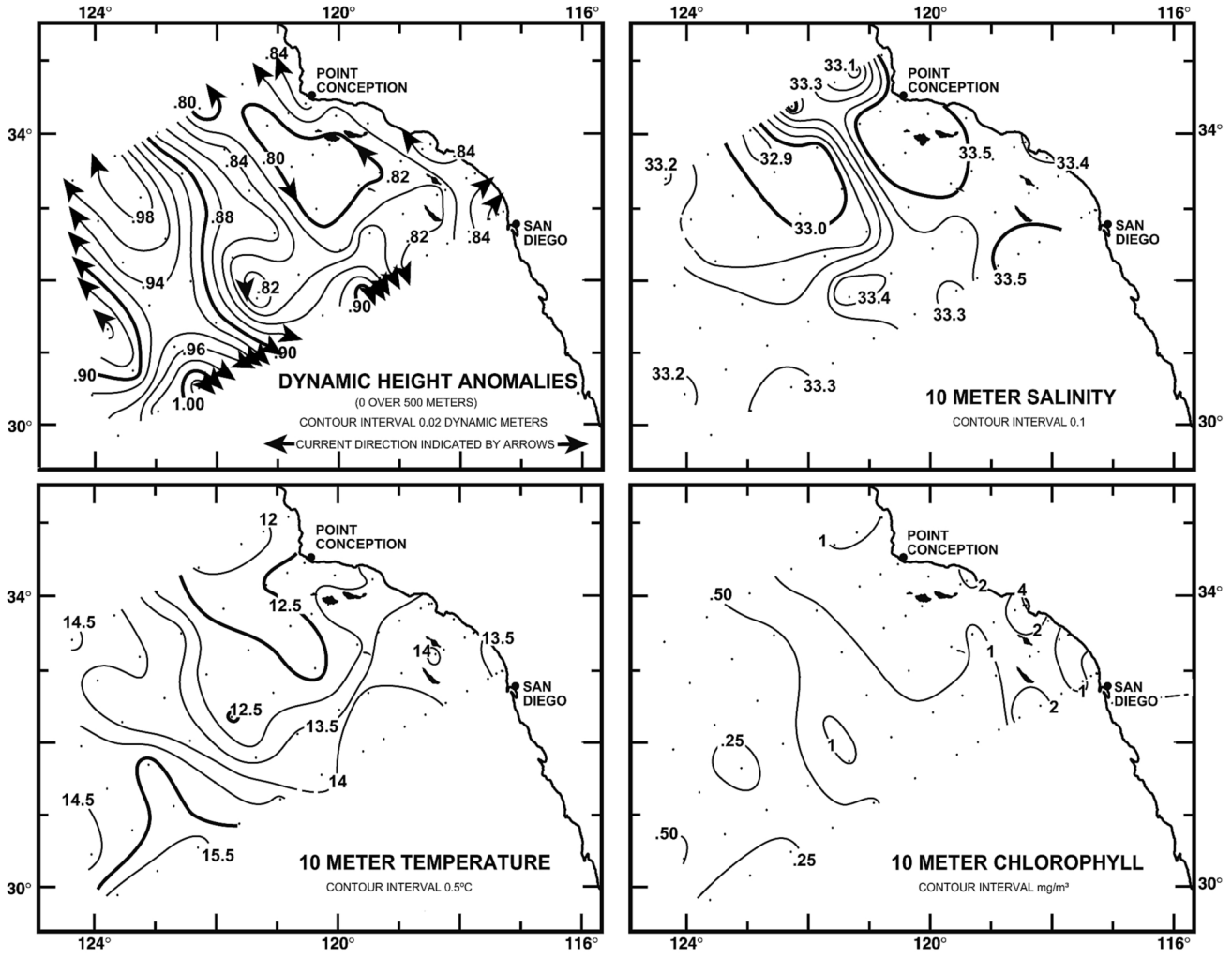

Figure 19. Spatial patterns for CalCOFI cruise 0801 including upper-ocean geostrophic flow estimated from the 0/500 dbar dynamic height field, 10 m salinity, 10 m temperature, and 10 m chlorophyll *a*. Data used for these plots are still preliminary.

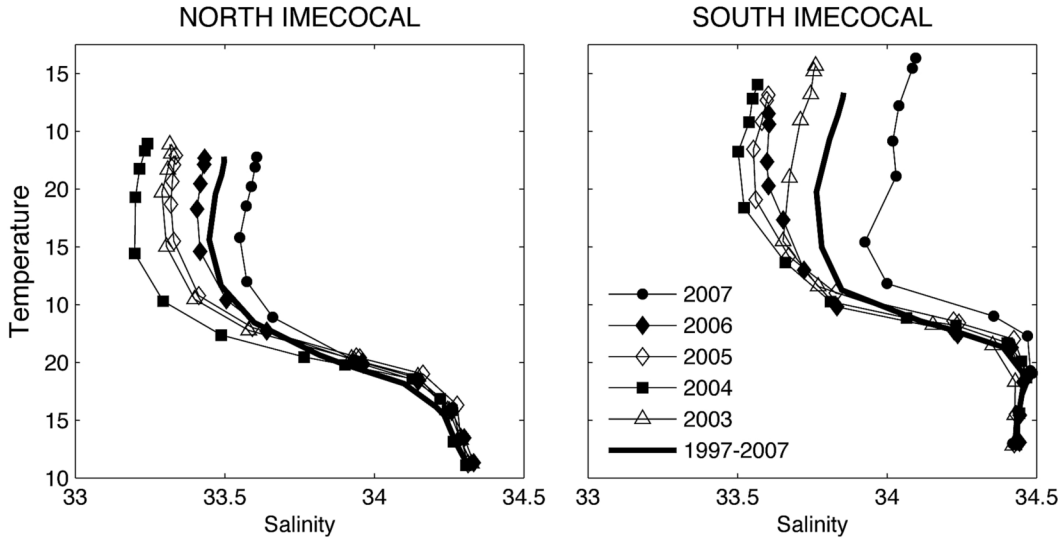

Figure 20. TS plots for the northern (A, Lines 100 to 110) and southern (B, Lines 123 to 130) sections of the IMECOCAL study area. Each data point represents the average TS characteristic of one standard depth level for the specified time periods, i.e., 1997–2007, 2003, 2004, 2005, 2006, and 2007.

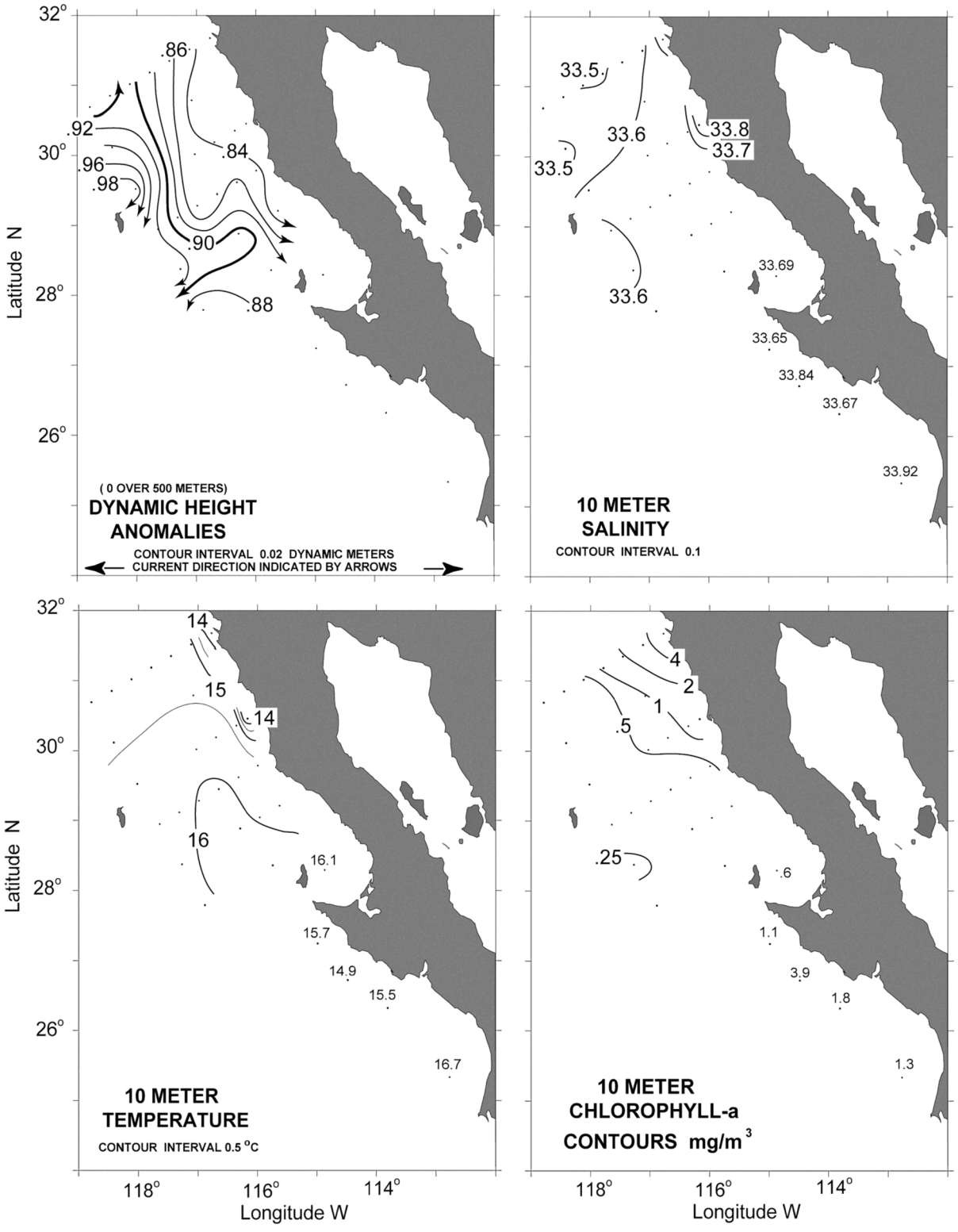

Figure 21. Spatial patterns for IMECOCAL cruise in spring 2007, showing upper ocean geostrophic flow estimated from the 0/500 dbar dynamic height anomalies, 10 m chlorophyll *a*, 10 m temperature, and 10 m salinity.

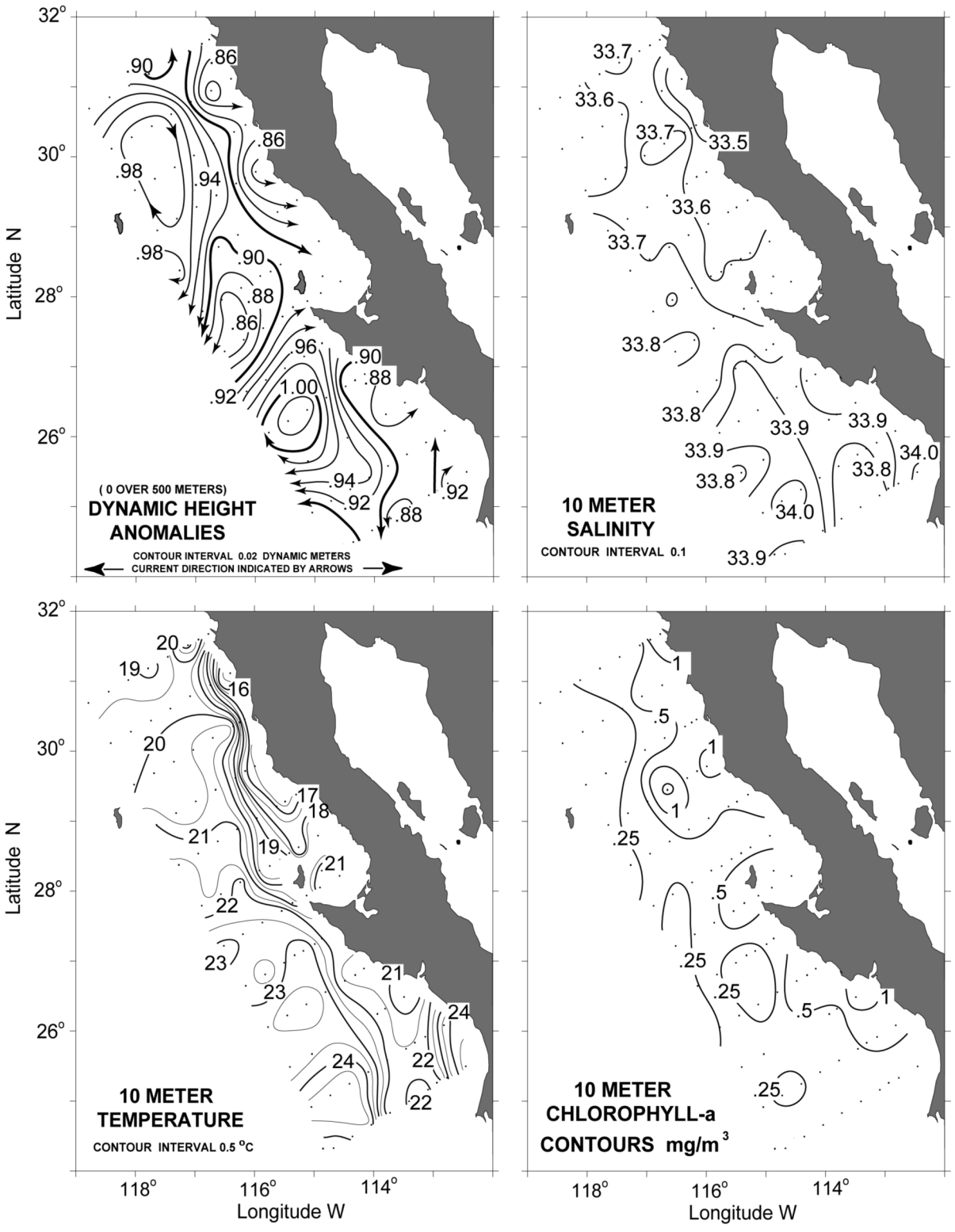

Figure 22. Spatial patterns for IMECOCAL cruise in summer 2007, showing upper ocean geostrophic flow estimated from the 0/500 dbar dynamic height anomalies, 10 m chlorophyll *a*, 10 m temperature, and 10 m salinity.

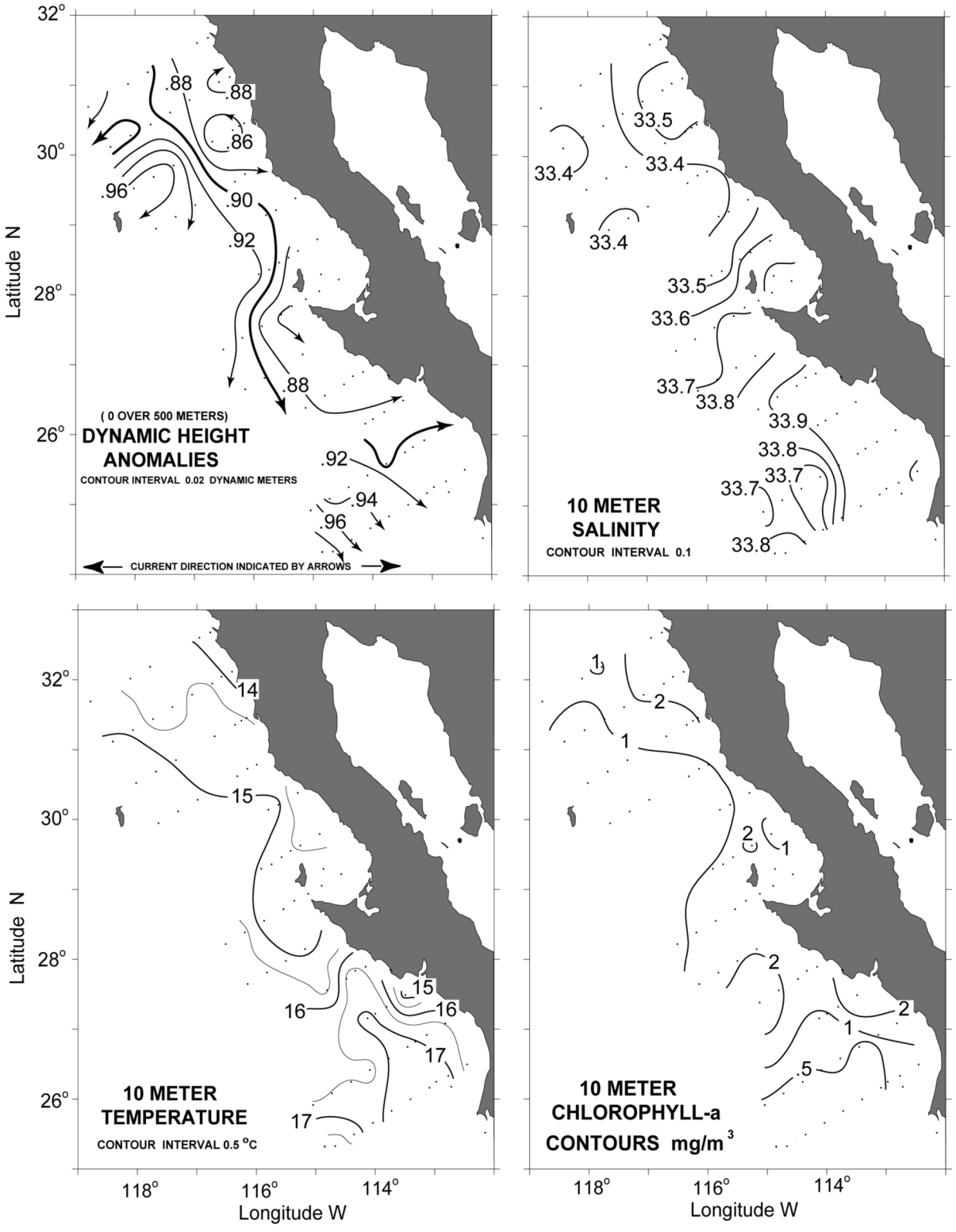

Figure 23. Spatial patterns for IMECOCAL cruise in winter 2008, showing upper ocean geostrophic flow estimated from the 0/500 dbar dynamic height anomalies, 10 m chlorophyll *a*, 10 m temperature, and 10 m salinity.

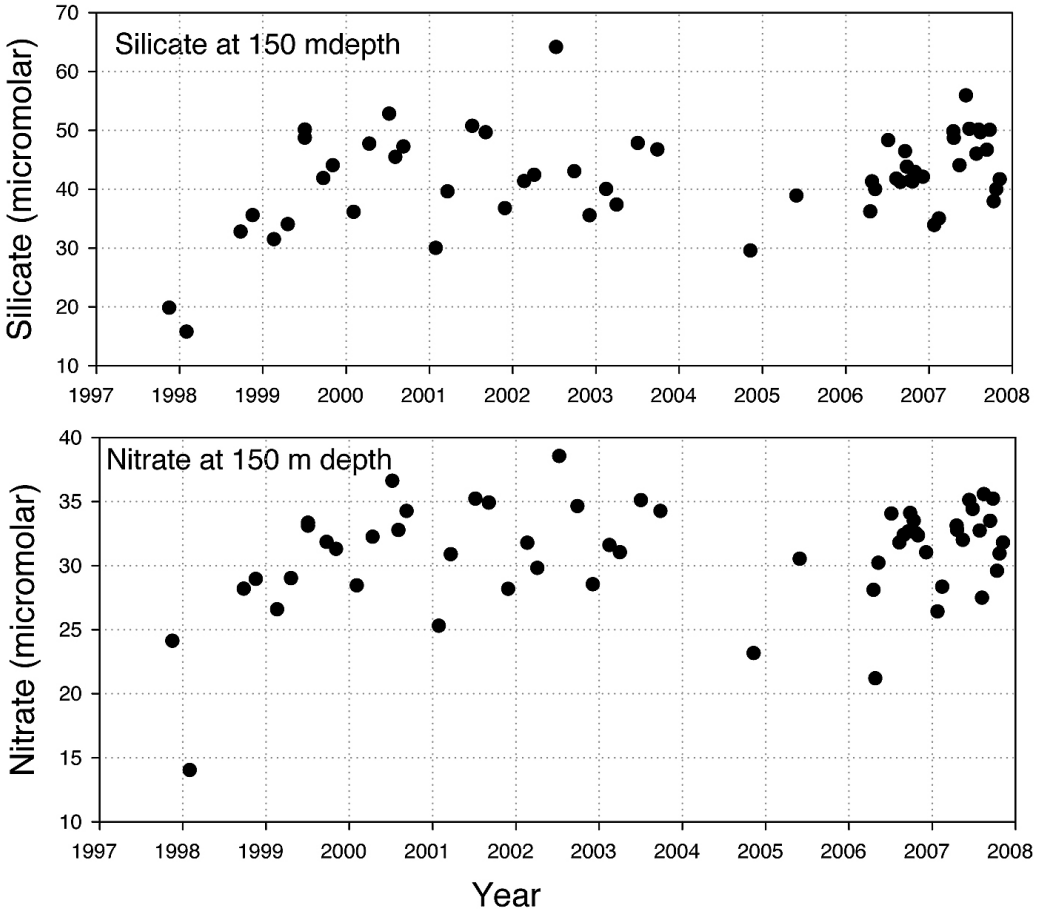

Figure 24. Time series of silicate and nitrate concentrations from station NH 25 (25 miles off Newport). Station depth is 300 m; sampling depth is 150 m.

branches at station 117.40. Between Ensenada (line 100) and San Quintin (line 107), relatively low temperatures and high salinities were encountered in the coastal areas, and show the effects of coastal upwelling. Phytoplankton chlorophyll *a* was high in these areas with values up to 4 μg/L, as is typical for these upwelling events.

IMECOCAL 0708
(25 August–14 September 2007; fig. 22)

Dynamic height anomalies depict a meandering California Current, with two large anticyclonic eddies at northern and southern locations, and a cyclonic eddy in between at ~28°N. As indicated by the relatively low salinities, the core of the current appears to be restricted to the northern region, both as part of the northern clockwise eddy and as nearshore flow. Coastal upwelling between Ensenada and Punta Baja is indicated by the relatively low temperatures (15°–17°C) and high chlorophyll *a* concentrations (>1 mg/m^3) near the coast in the northern region, while warmer (>21°C) and salty (>33.8 psu) conditions were observed in the southern region.

IMECOCAL 0801
(22 January–11 February 2008; fig. 23)

Similar to April 2007, bad weather during this survey did not permit sampling at some offshore stations. The flow pattern of the California Current in the northern section was similar to that observed during April 2007. The southern section was characterized by southeastward flows. Coastal upwelling likely occurred off Ensenada and in the south at ~29.5°N, where 10 m water temperatures less than 15°C and chlorophyll-*a* concentrations higher than 2 mg/m^3 were observed. Upwelling at this time of the year is atypical for these regions.

BIOLOGICAL PATTERNS AND PROCESSES

Macronutrients, Chlorophyll *a* and Primary Production

Oregon: Sea surface nitrate concentrations at NH 05 in spring 2007 (April–June) were 4.6 μM, about average for our 11-year time series (tab. 1). During July–August, despite the weak upwelling, nitrate con-

TABLE 1
Average nitrate (μM) and chlorophyll (μg chlorophyll *a* L^{-1}) concentrations measured at the sea surface at station NH 05, five miles off Newport, in spring (April–June) and summer (July–August) for the years 1997–2007.

	Nitrate (μM)		Chlorophyll *a* (μg chl *a* L^{-1})	
YEAR	April–June	July–August	April–June	July–August
1997	5.21	7.95	1.1	6.1
1998	1.91	2.25	2.2	10.5
1999	4.95	10.20	1.8	5.5
2000	8.65	12.00	1.9	8.4
2001	4.16	9.43	6.6	9.0
2002	4.28	11.49	6.1	10.9
2003	4.37	10.30	3.0	9.7
2004	3.62	8.41	4.9	8.1
2005	0.67	11.70	2.6	8.7
2006	10.1	11.74	2.2	10.1
2007	4.6	11.0	3.5	9.2

centrations were also about average, 11.0 μM. This suggests that despite the warm SST, there were a sufficient number of active upwelling events that surface nutrient levels were not anomalously low.

The chlorophyll-*a* values averaged for spring (April–June) and summer (July–August) 2007 were 3.5 μg/L and 10.1 μg/L respectively, similar to other years (tab. 1). This result would be expected with "average" nitrate concentrations and again suggests that although upwelling was weak, it was not so weak as to result in a lack of production.

Nitrate and silicate measured at a depth of 150 m at NH 25 are shown in Figure 24. One clear pattern is the increase in nitrate and silicate concentration from the 1997–98 El Niño period until 2000, after which there was a tendency towards relatively constant values for each nutrient: most recent values fall into the range of the long-term average of 30–35 μM for nitrate and 40–50 μM for silicate.

CalCOFI: Since the 1997–98 El Niño, nitracline depths have been approximately 5 m deeper than long-term averages, with values ranging from 31 to 49 m. Early in 2007 nitracline depth anomalies for the whole CalCOFI region were similar to those observed since 2000 (fig. 25); i.e., slightly deeper than long-term averages. In the fall of 2007 and winter of 2008 nitracline depths shoaled to extremely low values, 33 and 27 m, similar to the shallowest observed values during the strong La Niña of 1989. Consistent with shallow nitracline depths and stronger than usual southward winds in the area (fig. 6), mixed-layer concentrations of nitrate were elevated during 2007 and early 2008 (fig. 26A). In contrast, mixed-layer concentrations of silicate and phosphate were, when averaged over the seasons, close to long-term averages, albeit variable. Whereas concentrations of silicate covaried with mixed-layer salinity during the last eight years, no such covariation was apparent during the last year (fig. 26C).

Standing stocks of chlorophyll *a*, integrated from the surface to the bottom of the euphotic zone (fig. 27A), were similar to long-term averages, with the exception of the spring 2007 value, which was one of the lowest spring values on the record. Mixed-layer concentrations of chlorophyll *a* (data not shown) had the same pattern. The response of phytoplankton biomass to the cooling of the system was similar to what was observed during the spring of the La Niña Year 1989; in contrast, spring chlorophyll *a* during the La Niña Year 1999 was one of

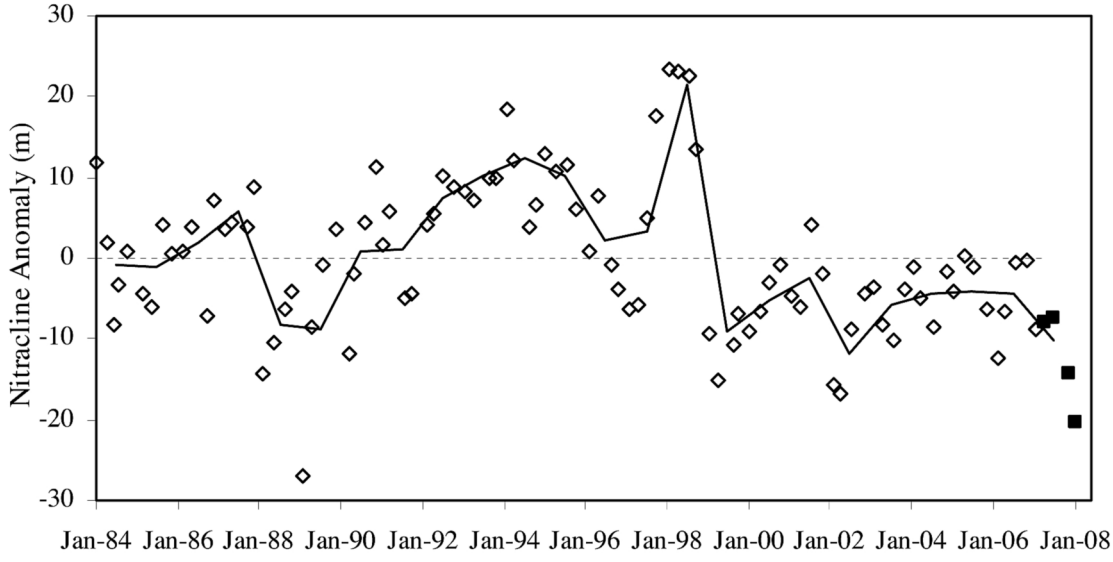

Figure 25. Cruise averages for nitracline depth anomaly. The nitracline depth was assumed to be the depth where nitrate reached values of 1 μM. Data are plotted as described in Figure 13.

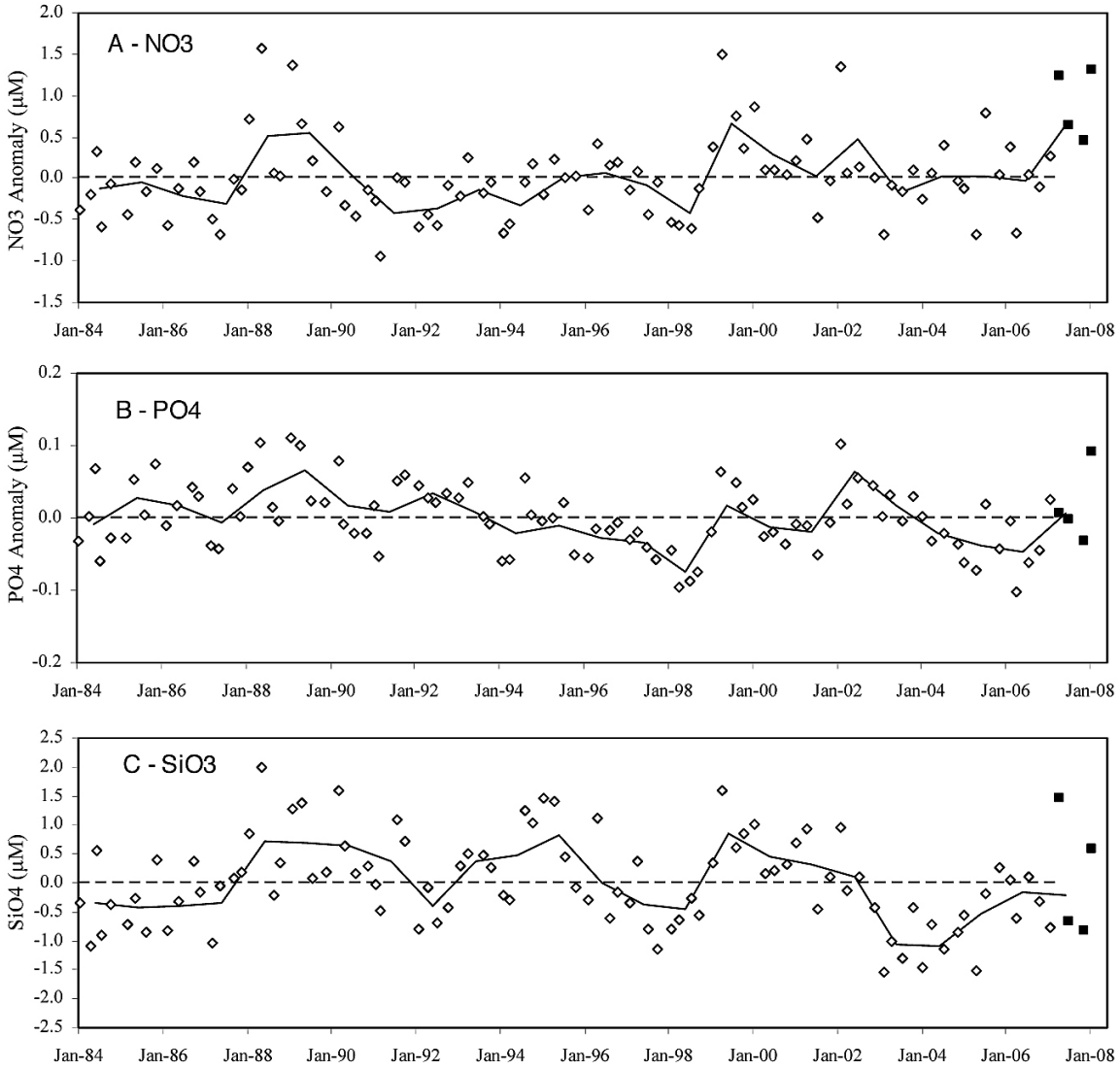

Figure 26. CalCOFI region anomalies for concentrations of (A) nitrate, (B) phosphate, and (C) silicate in the mixed layer. Data are plotted as described in Figure 13.

the highest on record. Rates of primary production were similar to long-term averages with the exception of those observed during the spring of 2007, which were below expected values (fig. 27B). Chlorophyll-*a* concentrations in all other areas were either above long-term averages (CC North and South and Edge of the Gyre; fig. 28A, B) or similar to these (Coastal South).

Zooplankton, Fish, and Seabirds

Oregon Zooplankton: The time series of copepod biomass (fig. 29) shows both a pronounced seasonal cycle with peaks in July/August, and pronounced interannual variations. Lowest averages for summer (May–September) were seen from 1996–99, and highest during the summers of 2000–04. The summer of 2005 had the lowest biomass of any summer, due to the delayed upwelling (Peterson et al. 2006). Biomass rebounded in 2006 and remained high through the summer of 2007.

Monthly-averaged copepod species richness was anomalously high throughout most of 1996–98, low from winter 1999–autumn 2002, then high from autumn 2002–spring 2006 (fig. 30). Richness anomalies turned negative in autumn 2006 and remained either negative or neutral through 2007. This pattern is similar to the pattern of PDO and MEI, suggesting that coherent patterns of PDO, SST, and copepod species richness may be related to transport processes in the northern California Current (NCC): anomalously low numbers of copepod species are associated with the transport of coastal subarctic water into the coastal waters of the NCC (as in

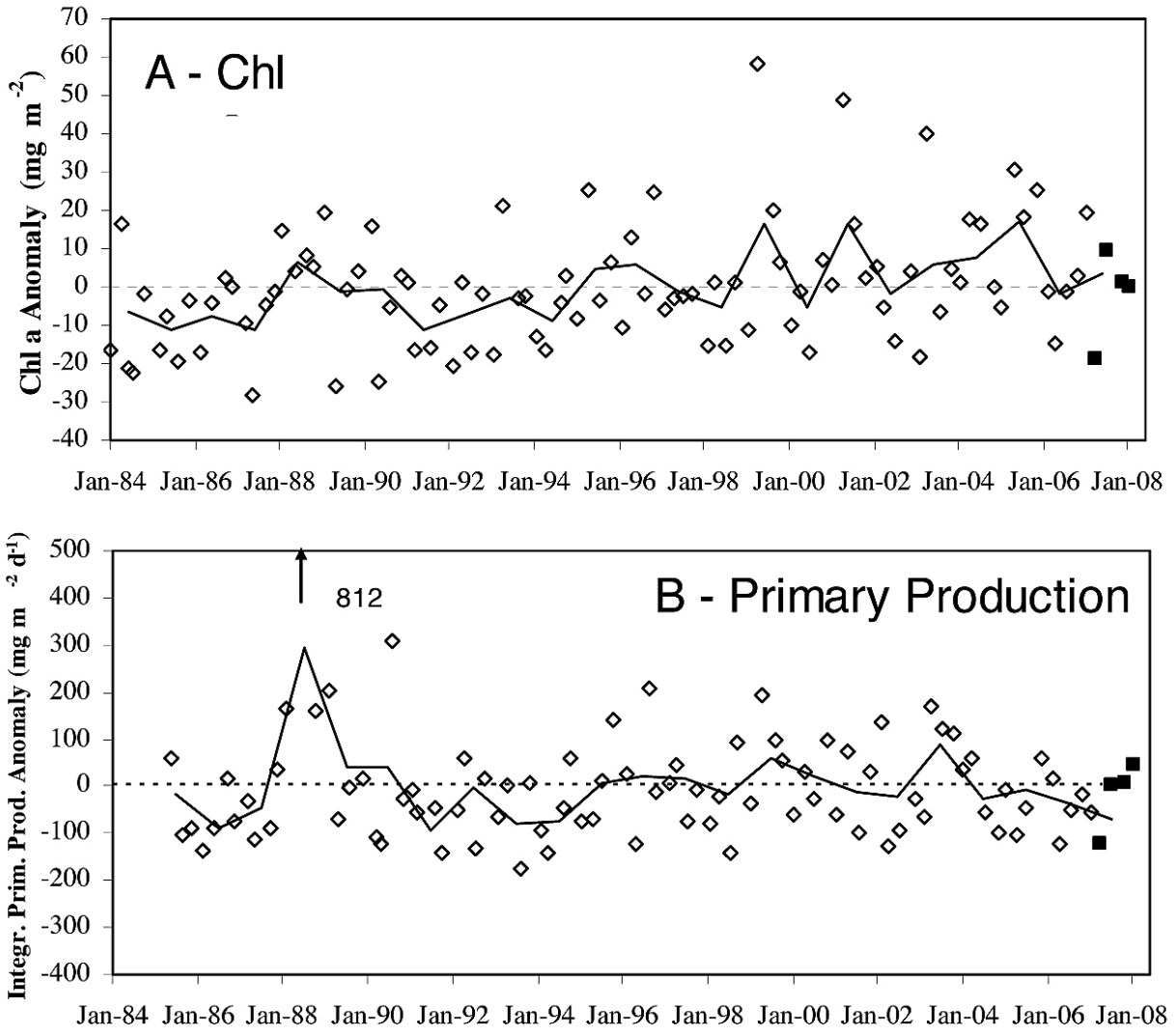

Figure 27. CalCOFI region averages for (A) standing stocks of chlorophyll *a* and (B) rates of primary production both integrated to the bottom of the euphotic zone, plotted against time. Data and symbol codes are the same as those in Figure 13.

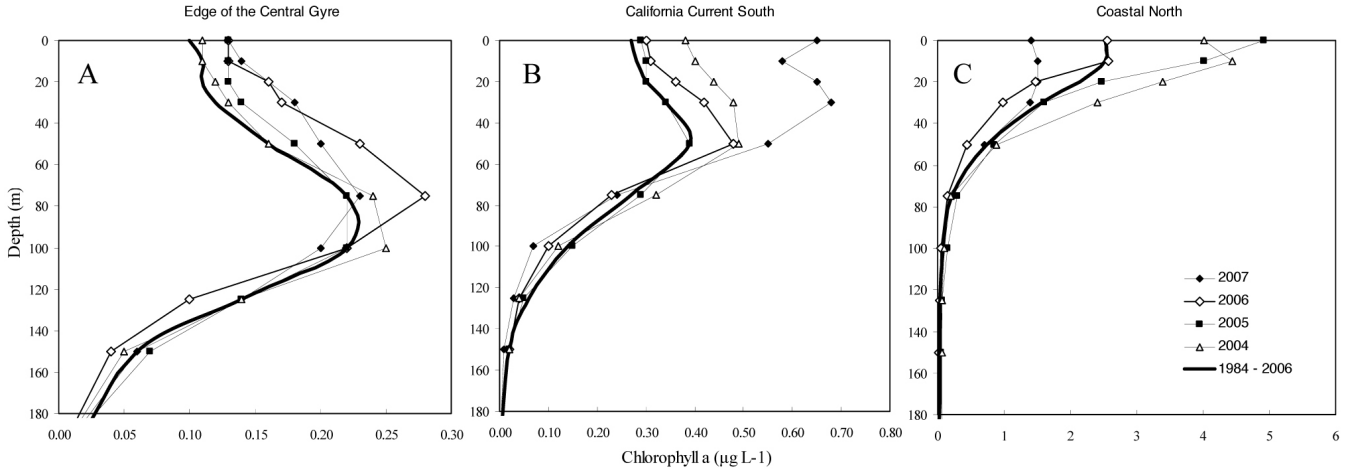

Figure 28. Depth profiles of chlorophyll *a* for the three areas of the CalCOFI region that were described in Figure 15, (A) the edge of the central gyre, (B) the southern California Current region and (C) the northern coastal areas (C). Data were calculated and are presented as described in Figure 15.

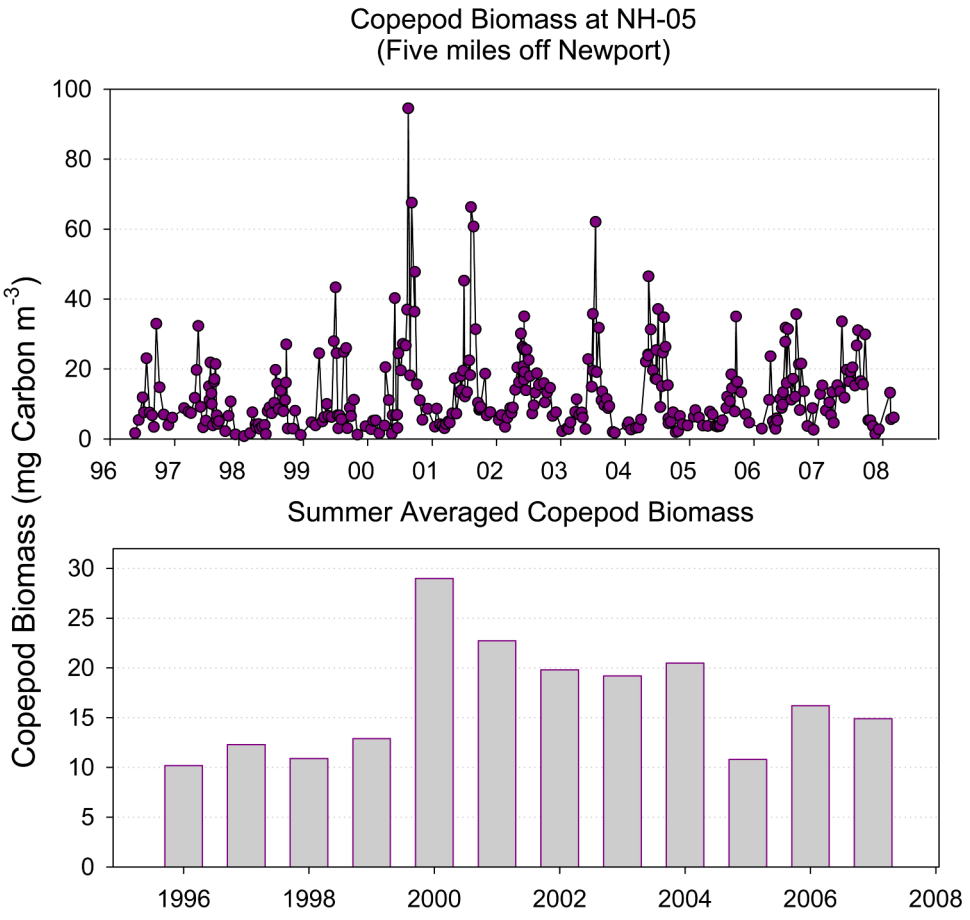

Figure 29. Newport Time series of monthly-averaged values of copepod biomass measured at a mid-shelf station, NH 05, from 1996–present, along with summer-averaged values of copepod biomass measured at NH 05.

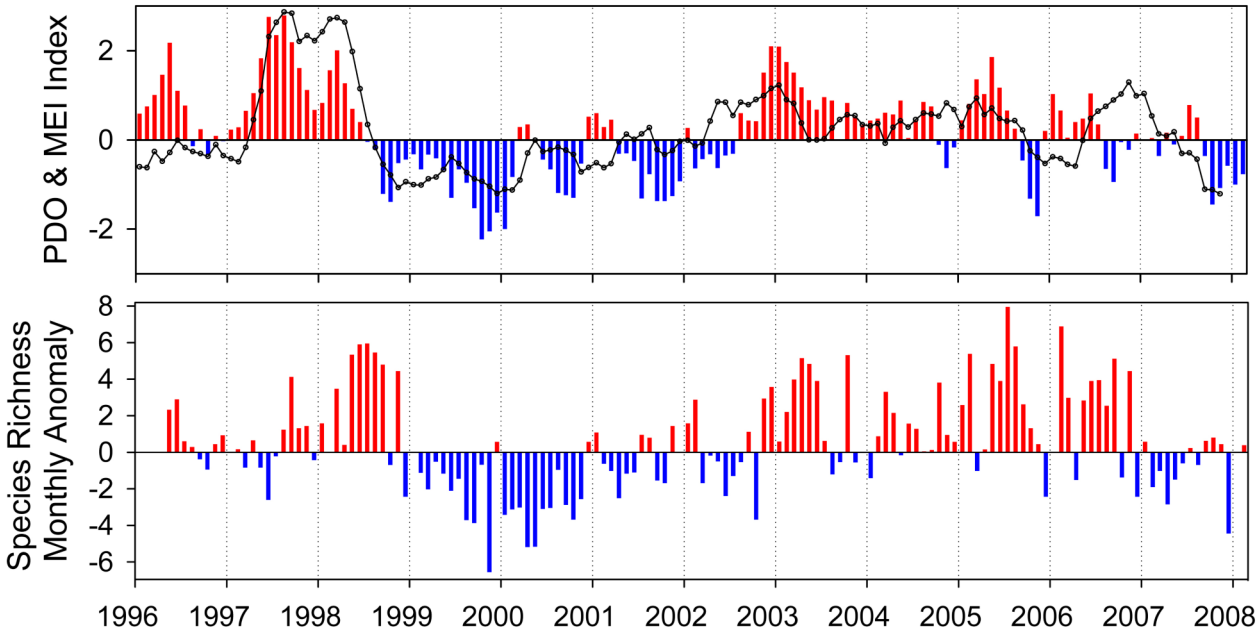

Figure 30. Time series of the Pacific Decadal Oscillation (upper panel, bars), Multivariate ENSO index (upper panel, line), and monthly anomalies of copepod species richness at station NH-05, from May 1996 through February 2008.

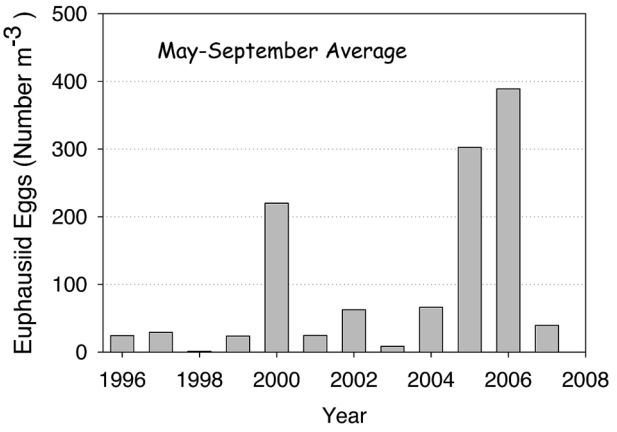

Figure 31. Time series of euphausiid eggs at NH 05, from 1996 through 2007. Note the extraordinary peaks in summer 2000, 2005, and 2006. Egg abundances were low in 2007.

1999–2002), whereas anomalously high numbers of species are associated with either a greater amount of onshore transport of warm, offshore, subtropical water, or northward transport of subtropical coastal neritic water along a coastal corridor (as in late 2002 to early 2006). See Hooff and Peterson (2006) for details.

The interannual variability in euphausiid egg abundances at station NH 05 (fig. 31) is very high; seasonal averages of egg abundances range over an order of magnitude among years. Highest abundances were seen in summers of 2000, 2005, and 2006. We attribute the enhanced egg concentrations in these years to higher numbers of adults in coastal waters during summer months. Low numbers suggest the absence of adult females in coastal waters.

CalCOFI Zooplankton: Macrozooplankton displacement volumes were slightly below long-term averages for the respective seasons in the spring and summer of 2007 and the winter of 2008. These were slightly above long-term averages during the fall of 2007 (fig. 32). Average macrozooplankton displacement volumes for 2007 continued the significant trend of declining zooplankton displacement volumes observed for the time period 1984 to 1998 and 1999 to 2007 (Goericke et al. 2007), with slopes for the two time periods which are virtually identical, -0.00020 and -0.00021 (± 0.00004 and 0.00005, respectively, fig. 32B).

Washington Forage Fish: Forage fish densities continued to follow the same trend as in 2006 of very low

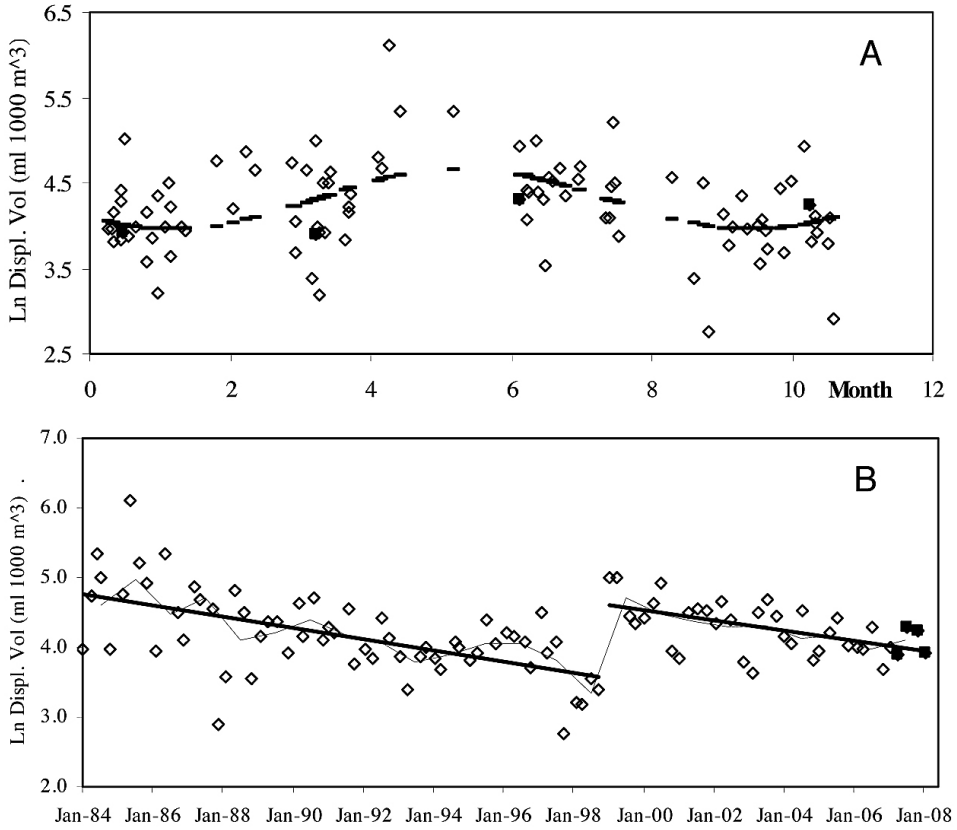

Figure 32. The natural logarithm of CalCOFI cruise-mean macrozooplankton displacement volumes (Ln Displ. Vol.) plotted against the month of the year (A), and the year (B). Annual averages are connected by thin solid lines. Results of regressions of Ln displacement volumes against time for the periods 1984 to 1997 and 1998 to 2006 are shown using the two straight lines.

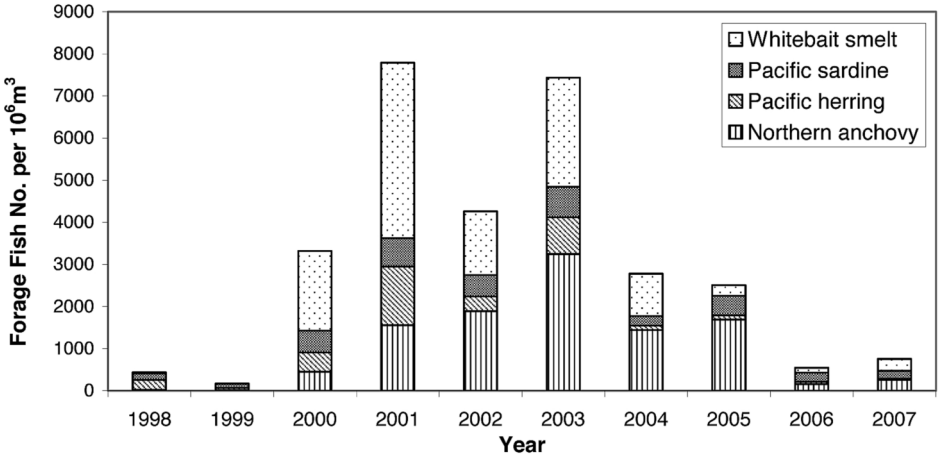

Figure 33. Forage fish densities averaged from rope trawls taken biweekly from May–August 1998 to present.

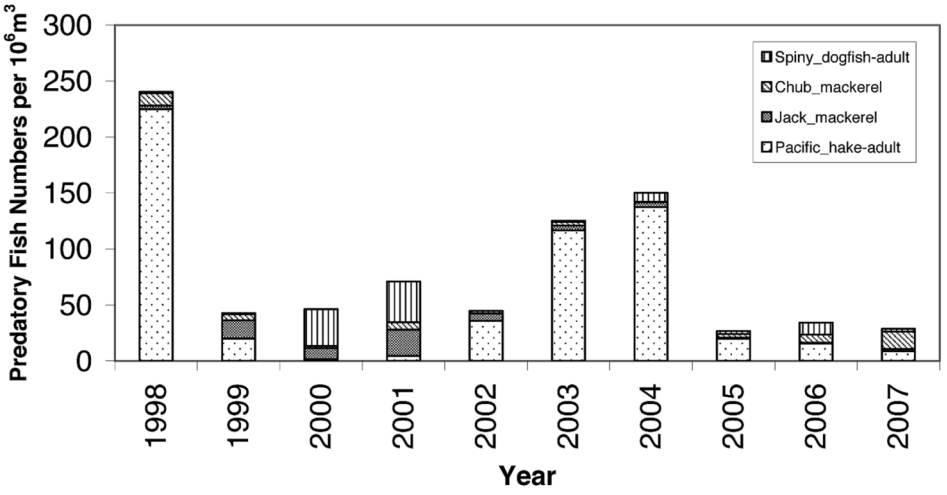

Figure 34. Predatory fish densities averaged from pelagic rope trawls taken biweekly from May–August 1998 to present.

abundances (fig. 33). This may have been due in part to low abundances of northern copepod species, which appears to be unfavorable for smelts, Pacific sardines, herring (*Clupea pallasi*), and northern anchovy. Highest abundances of forage fish were seen in 2000–03, and followed closely the four-year period of negative PDO in 1999–2002, but with a one-year lag.

Washington/Oregon Predatory Fish: Until recently, catches of predatory fish appeared to be related to warm ocean conditions—that is, highest numbers were found in shelf waters during the 1998 El Niño, and during the warm period 2003 and 2004. However, although warm conditions prevailed through 2005 and 2006, numbers of predatory fish declined in our pelagic rope trawl surveys (fig. 34). We have no explanation for this. Not shown in this graph are the high numbers of one-year-old Pacific hake (*Merluccius productus*) observed in 2007. These were 0-age in 2006 and were reported on by Phillips et al. (2007) at the 2006 CalCOFI meeting. Based on the recent occurrence of larval hake off Oregon and Washington and increased abundance of Age 0 and 1 fish, it seems likely that Pacific hake are now spawning in the northern California Current (Phillips et al. 2007).

CalCOFI Fish Spawning: In spring 2007, as in spring 2005, the eggs of Pacific sardine and jack mackerel were not as abundant as in other recent years. This was in contrast to the more abundant northern anchovy eggs (fig. 35). Sardine eggs were widely distributed, and most abundant between San Diego and Avila Beach (fig. 35). Sardine eggs were less abundant in the north, which was also the case in spring 2004. Anchovy eggs were confined to the Southern California Bight, and jack mackerel eggs were found offshore of the sardine eggs, with relatively little overlap, as found in many other years. The area between Avila Beach and Monterey was not sampled as planned due to weather conditions.

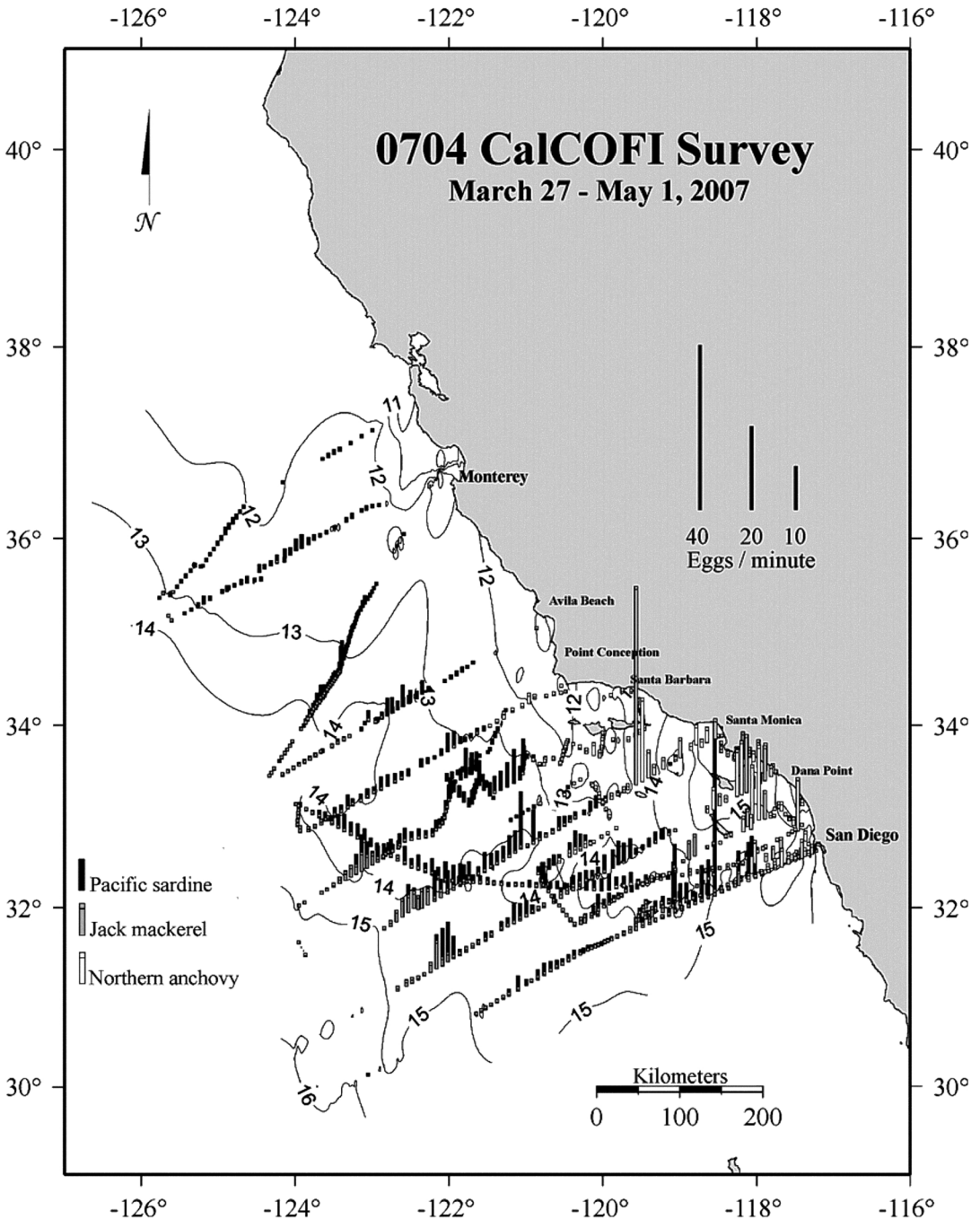

Figure 35. Rate of occurrence of eggs of Pacific sardine (*Sardinops sagax*), northern anchovy (*Engraulis mordax*), and jack mackerel (*Trachurus symmetricus*) sampled with the continuous underway fish egg sampler (CUFES) and sea surface temperatures in 27 March–1 May 2007. One egg per minute corresponds to approximately 6.6 eggs per cubic meter (Note the ratio may vary from year to year).

Overall, the eggs of sardine and anchovy were more abundant than jack mackerel eggs.

In 2007 Pacific sardine eggs were found in temperatures between 10.1°C and 15.6°C. The weighted mean sea surface temperature was 13.8°C for the area occupied by the standard DEPM survey as compared to 14.95°C in 2006, 14.21°C in 2005, 13.4°C in 2004, and 13.7°C in 2003.

The spawning biomass of Pacific sardine is a fishery independent population index, and it is useful to see how the spawning related to the sea surface temperature in the past years based on CalCOFI surveys (Lo et al. 2007).

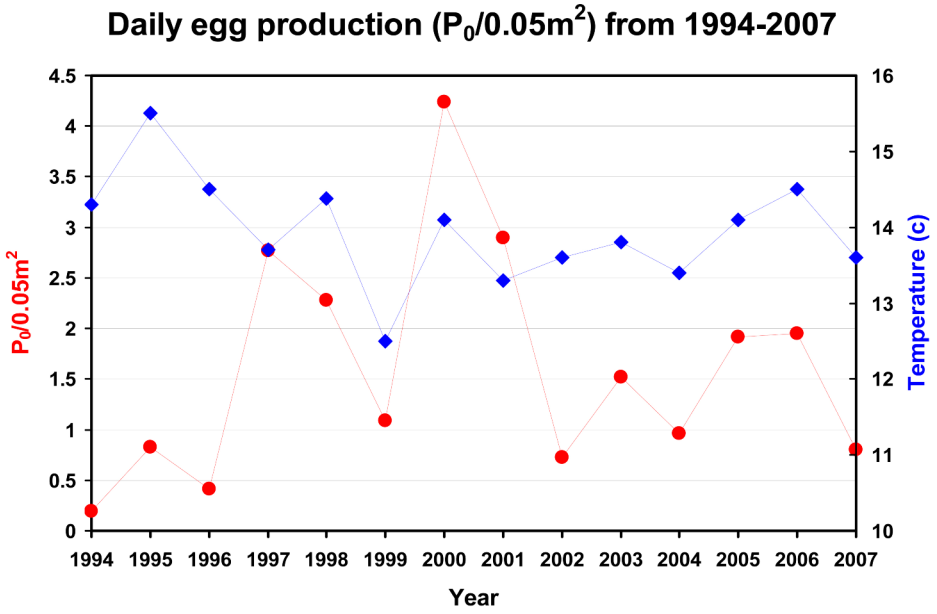

Figure 36. Daily egg production/0.05m^2 of Pacific sardine (circle) and average sea surface temperature (°C) (diamond) during March–April CalCOFI cruises from 1994–2007.

The spawning biomass of Pacific sardine is related to the daily egg production to some degree, in particular if the number of oocytes per biomass weight remains constant (Lo et al. 2005). The relationship between the daily egg production /0.05 m^2 and the average sea surface temperature (°C) during 1994–2005 indicated that in most years, except in 1997 and 2002, the increase of daily egg production coincides with the increase of sea surface temperature (fig. 36). This relationship is consistent with the assertion that high temperature is favorable for the Pacific sardine (Jacobs and MacCall 1995), in particular in recent years (after 2000, fig. 36).

CalCOFI Larval Fish and Squid in Relation to Oceanographic Features: In April 2007 the surface oceanography of the Southern California Bight showed strong physical features created by processes that were likely to affect the spatial distribution of larval fish. The important physical features (c.f. fig. 16) were two semi-coastal features in the northern (33.2°–34.5°N, 120°–122°W) and southern (32°–33.5°N, 117°–118°W) parts of the CalCOFI study area and the core of the California Current running roughly parallel to the coast (121°–123°W) with a meander at approximately (31°–33°N, 122°–124°W). Between these three features was a region of lower flows in the upper 200 m as well as a weak cyclonic eddy centered on station 83.80. Distributions of the Pacific sardine (*Sardinops sagax*) and market squid (*Loligo opalescens*) are discussed here in relation to this physical structure.

Pacific sardine larvae were anomalously high in abundance in spring 2007, but this anomaly was largely restricted to an approximately 50 km (east-west) by 150 km (north-south) area (fig. 37). The southern area of high sardine larval abundance was associated with the inshore edge of the California Current south of 31°N, and the northern area of high sardine larval abundance was associated with the region of low dynamic height gradients, east of the small cyclonic eddy at station 83.80. The sardine larvae were in a region of quite homogeneous temperature (approximately 14°–14.5°C) and salinity (33.4–33.45). The concentration of sardine larvae was associated with a minor positive anomaly in small zooplankton displacement volume.

A market squid paralarval concentration was found much closer to shore (200–300 km offshore along line 90) compared to the sardine larvae (400–500 km offshore), but were certainly not in the nearshore zone. The paralarvae were small, no more than a few days old, and the high concentration at station 90.53 was in the vicinity of the Tanner-Cortez Bank, not far from shallow water and potential squid spawning habitat (and a place where it is not unusual to find shorefish larvae). A second lower concentration at station 80.55 is just outside the mouth of the Santa Barbara Channel, where paralarvae might have been transported from the San Miguel-Santa Rosa spawning grounds. Squid were in slightly cooler water (13.5°–14°C) and slightly saltier water (33.45–33.5) than the sardine larvae (see fig. 16).

In summary, for 2007 the anomalies of Pacific sardine larvae were both related to well-defined oceanographic features. Sardine anomalies were positive in relation to the offshore edge of an eddy feature and to the inshore

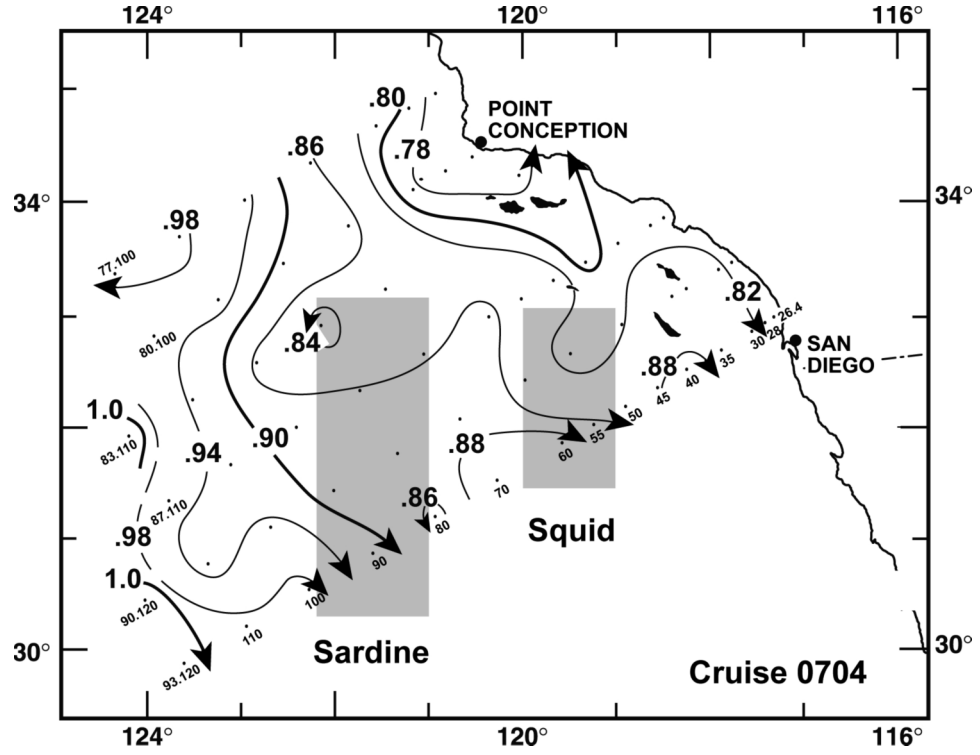

Figure 37. Dynamic height anomaly contours at 25 m referenced to 200 m indicating near-surface geostrophic flows. Shaded boxes show the location of positive anomalies in Pacific sardine (*S. sagax*) abundance (offshore) and market squid (*L. opalescens*) abundance (inshore).

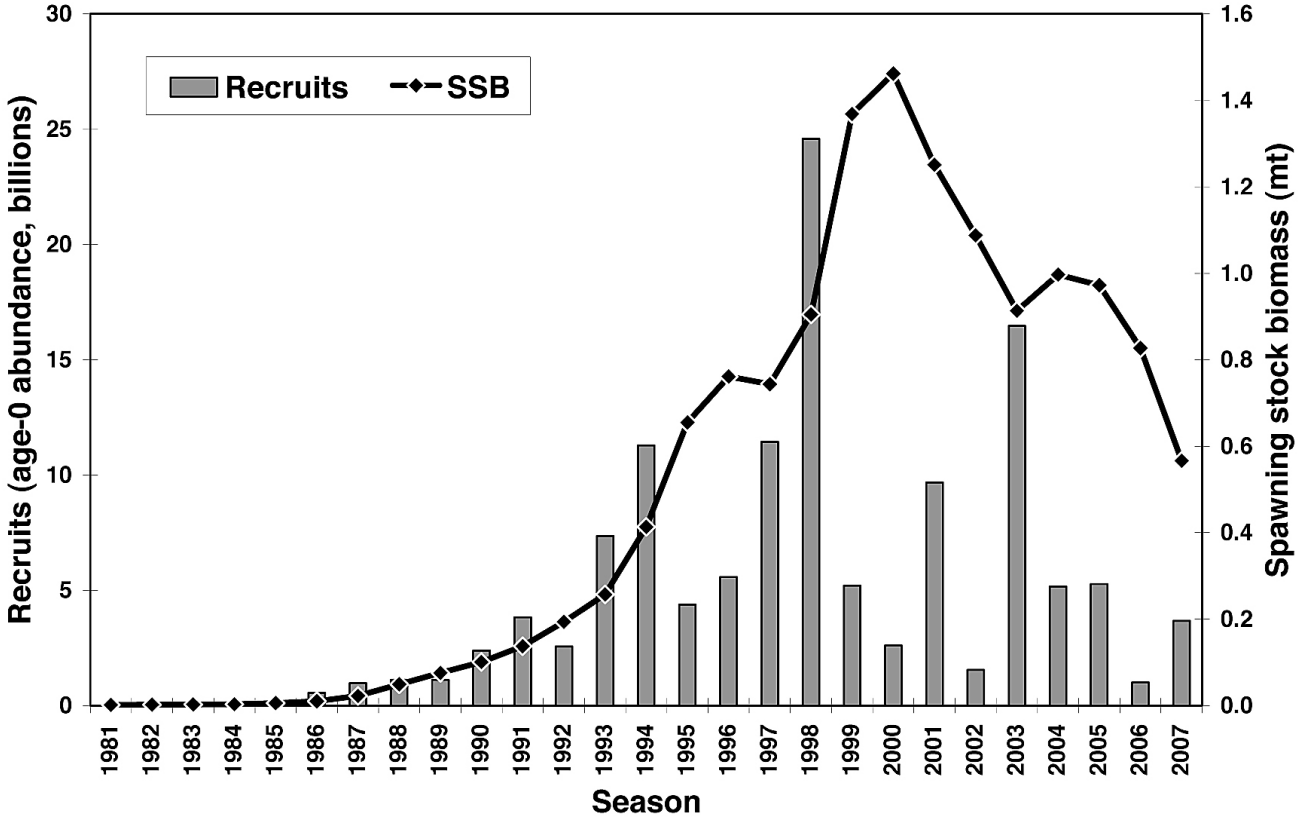

Figure 38. Pacific sardine spawning biomass and recruitment estimates from the Stock Synthesis 2 integrated assessment model.

edge of the California Current. Market squid paralarvae showed less relation to oceanographic structure and may have reflected proximity to spawning habitat.

Trends in Pacific Sardine Spawning Biomass and Recruitment: The SWFSC assesses the Pacific sardine population annually in support of the Pacific Fishery Management Council's process for establishing harvest limits for the U.S. fishery. The latest population assessment (Hill et al. 2007), based on the fully-integrated model Stock Synthesis 2 (SS2; Methot 2005), incorporated a time series of spawning stock biomass from the egg production surveys conducted each spring between San Diego and San Francisco (Lo et al. 2007), as well as 27 years of catch, size, and age composition data from fisheries occurring between Ensenada and British Columbia.

SS2 model estimates of recruitment (year-class abundance) and spawning stock biomass are presented in Figure 38 (Hill et al. 2007). Recruitments increased rapidly from the early 1980s through the 1990s, peaking at 24.6 billion age-0 fish in 1998. Recruitments have been relatively lower since 1999, with the exception of the 2003 year class, which was the second highest in recent history (16.5 billion fish). As a result of declining year-class production, sardine spawning stock biomass, which peaked at 1.46 million mt in 2000, has since trended steadily downward.

Reasons for declining sardine production since the late 1990s are currently unknown. Exploitation by the combined fisheries is relatively low (about 15%), so overfishing is an unlikely explanation for the decline. The Scripps Pier based temperature criterion for the sardine harvest guideline remains high (see Hill et al. 2007).

Avifauna: CalCOFI research cruises have provided the opportunity to relate fluctuations in marine bird community structure to changes in physical and biological attributes of the California Current large marine ecosystem over inter-annual and longer temporal scales (Hyrenbach and Veit 2003; Yen et al. 2006). Colony-based studies of seabird reproductive performance and diet have also documented coupled climate-ecosystem fluctuations at multiple temporal scales (Sydeman et al. 2001; Mills et al. 2007). Herein we place these recent observations (2007) of seabird reproductive performance and community structure at-sea in the context of the conditions experienced since the transition from a warm to a cold regime of the Pacific Decadal Oscillation (PDO) in the late 1990s (Bograd et al. 2000).

Most recently, summer-time CalCOFI surveys and colony-based studies have documented unprecedented breeding failures and nest abandonment by planktivorous auklets on the Farallon Islands (central California), in response to unusual atmospheric and oceanographic conditions in 2005 and 2006 (Sydeman et al. 2006; Goericke et al. 2007). To interpret the oceanographic mechanisms responsible for these auklet responses, we investigate the response of planktivorous auklets to basin-scale (north Pacific Ocean) and regional-scale (CCS) environmental conditions using a nine-year time series (1999–2007).

Farallon Island Seabird Productivity: We have observed seabird productivity for six species breeding at southeast Farallon Island (SEFI) for 36 years (1971–2006). To illustrate life-history variation, we have grouped species according to basic reproductive patterns: those producing a single egg clutch (Cassin's auklet *Ptychoramphus aleuticus*, common murre *Uria aalge*, rhinoceros auklet *Cerorhinca monocerata*) and those producing multiple-egg clutches (Brandt's cormorant *Phalacrocorax penicillatus*, pigeon guillemot *Cepphus columba*, pelagic cormorant *Phalacrocorax pelagicus*).

All six marine bird species experienced an increase in reproductive success from the previous year (2006), even though four species experienced negative anomalies well below the long-term (1999–2007) mean (fig. 39). Only the Brandt's cormorant and the common murre performed at a level exceeding the baseline of the last nine years. Most notably, the Cassin's auklet experienced a recovery in reproductive success (0.31 chicks per breeding pair) after two years of complete failures (0.00 chicks per breeding pair) in 2005 and 2006. Yet, this value falls well below the long-term (36-year) average of ~0.7 chicks per pair (Sydeman et al. 2001, 2006) and the reproductive success experienced in recent "normal" periods (0.83 chicks per breeding pair in 1999–2000), and in very productive years when some birds raised more than one chick (1.11 chicks per breeding pair in 2001–02; fig. 39).

Clustering of seabird productivity data over the nine-year period revealed three distinct clusters. The current year (2007), clustered with the last two years of breeding failures (2005, 2006; fig. 40), and contrasted sharply with the first two years (1999, 2000) of high seabird productivity for all species. Three years of intermediate productivity (2001, 2002, 2004) clustered together, despite inter-annual fluctuations. The only year that stood out alone was 2003, a warm-water year characterized by depressed reproductive success for all six seabird species monitored.

Seabirds at Sea in the CalCOFI Region: To illustrate fluctuations in marine bird communities, we focus on three sub-arctic species, indicative of cold-water conditions in the CCS: the locally-breeding Cassin's auklet and common murre and the sooty shearwater (*Puffinus griseus*), a spring–fall visitor from the southern hemisphere (fig. 41). The at-sea abundances of the shearwater, murre, and auklet have declined in the southern CCS over the long-term (1987–98), despite incursions during cold-water years (Hyrenbach and Veit 2003; Bograd et al. 2000).

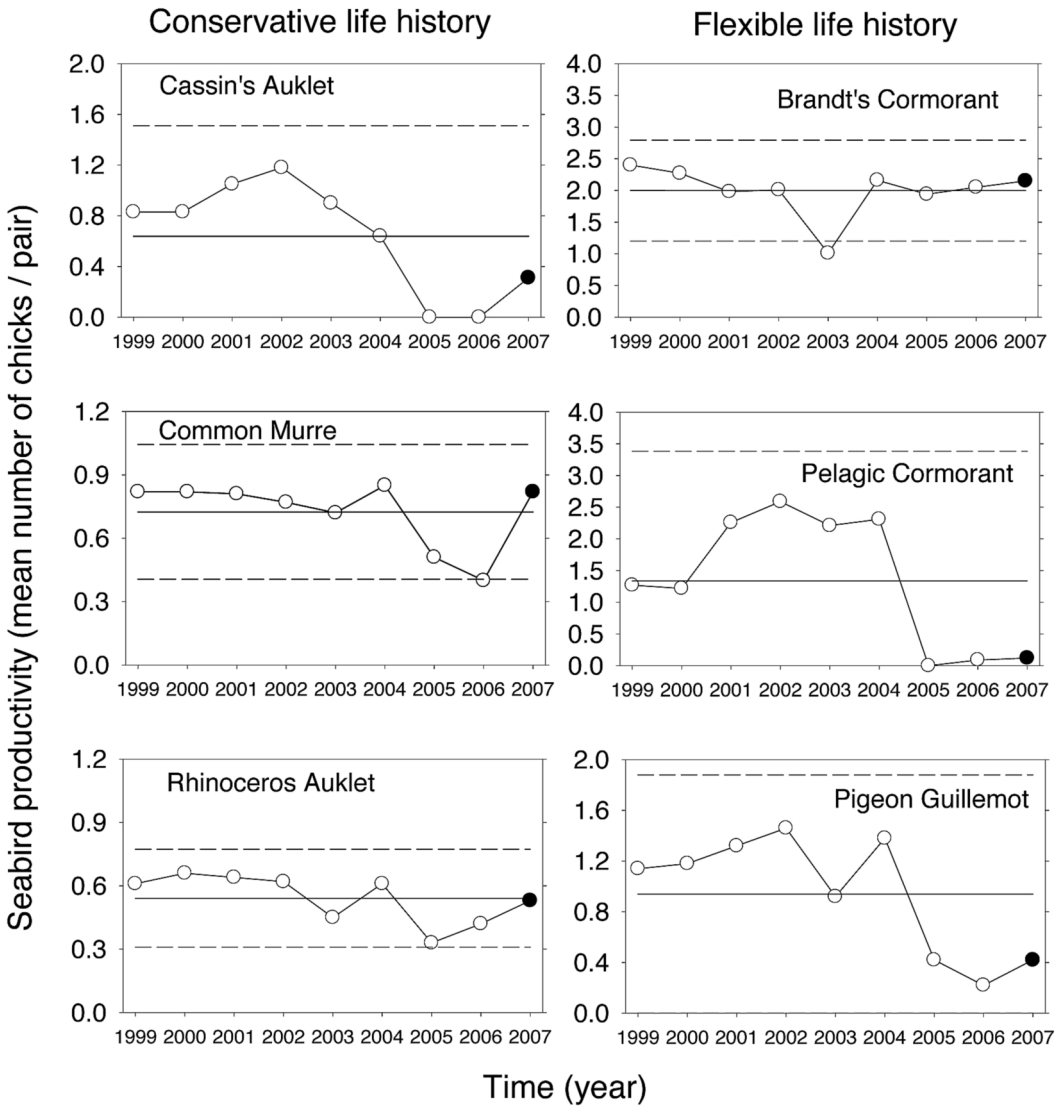

Figure 39. Productivity of six seabird species breeding at the Farallon Islands (37° 42'N; 123° 00'W). The long-term average (1999–2007) productivities are depicted by the solid horizontal lines, and the hatched lines illustrate the year-to-year variability (mean + 2 S.D.). Filled circles highlight productivity values in 2007.

More specifically, to investigate the extent of the Cassin's auklet post-breeding redistribution southwards into the Southern California Bight, we focus on summer-time (July) CalCOFI–CCE LTER cruises. The summer densities of the sooty shearwater and the common murre were anomalously low in 2007 (fig. 41). Only the auklet abundance was anomalously high, reaching the highest value observed since 1999.

Responses of Planktivorous Auklets: Together, the two dominant principal component (PC) factors explained 65% of the observed variance. The first factor was characterized by positive loading of auklet density at sea, positive loading of upwelling indices (winter, early spring, late spring), and negative loadings of MEI and PDO (in early and late spring). This PC underscores the links between regional upwelling dynamics, basin-wide atmospheric and oceanographic processes, and seabird distributions at sea. The second PC, which was characterized by contrasting loadings of auklet at sea abundance (positive) and productivity (negative), had positive MEI and PDO loadings (late winter, early spring, late spring). Most notably, late spring (May–June) upwelling at 36°N had a large negative loading, highlighting the importance of local productivity to auklets breeding off central California (SEFI).

Avifauna Conclusions: In 2007, the reproductive performance of Farallon seabirds was better than in 2005 and 2006 (fig. 39). Surprisingly, 2007 clustered with the two preceding years of breeding failures (2005 and 2006) (fig. 40), even though we found anomalously high at-sea

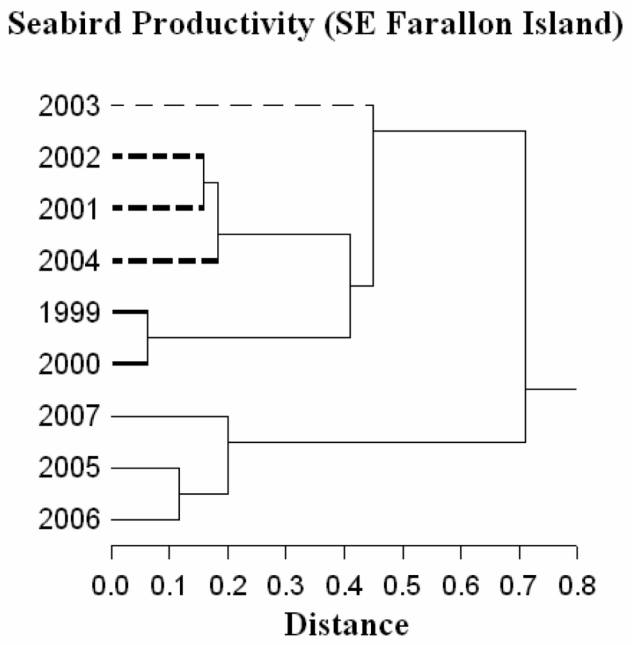

Figure 40. Cluster tree of marine bird productivity for the seabirds breeding on the Farallon Islands. The Euclidean distances are based on the hierarchical clustering technique, with the median linkage algorithm. The thickness and hatching of the lines identify those years in the same cluster.

densities of planktivorous auklets for the third summer in a row (fig. 41). Despite the concurrent increase in auklet reproductive success and at-sea abundance in 2007, these two metrics remain negatively correlated across the time series (Spearman rank, rs = –0.65, n = 9). This result underscores the notion that large numbers of auklets disperse southwards into the CalCOFI region in years of poor reproductive success and high nest abandonment (Sydeman et al. 2006). Furthermore, the PCA highlights the responses of planktivorous auklets to basin-wide and regional-scale oceanographic variability. We contend that the observed changes in colony productivity and at-sea distributions are mediated by shifts in the regional availability of prey resources, in this case the abundance of the euphausiids *Thysnoessa spinifera*, *Euphausia pacifica*, and *Nyctihanes simplex*.

DISCUSSION

The California Current system (CCS) has overall been in a cool phase since the 1998–2000 ENSO event. A variety of system parameters responded strongly to this forcing. Examples of the parameters that responded strongly to this "regime shift" are SST in many areas of the CCS (e.g., Monterey, fig. 10A, CalCOFI area, fig. 13 A), nutricline depth in the CalCOFI area (fig. 25), concentrations of chlorophyll *a* in Monterey Bay (fig. 10C), and zooplankton displacement volume in the CalCOFI area (fig. 32). Current values of these parameters suggest that this basic state of the system has not changed.

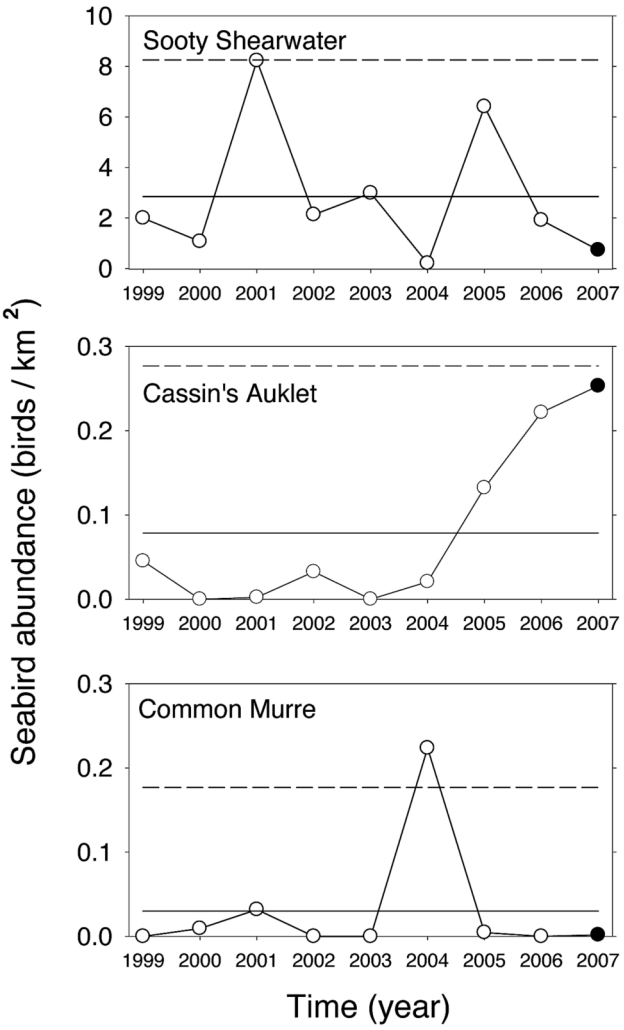

Figure 41. At-sea abundance of three seabird species with an affinity for cold-water conditions during summertime CalCOFI–CCE LTER cruises. The long-term average (1999–2007) densities are depicted by the solid horizontal lines and the hatched lines illustrate the year-to-year variability (mean + 2 S.D.). Filled circles highlight abundances in 2007.

The El Niño of 2006 was of moderate strength in the equatorial Pacific but had little effect on the CCS (Goericke et al. 2007). El Niño conditions ended in early 2007 and since the late spring of 2007 various indicators displayed La Niña conditions (e.g., the NINO 3.4 indicator, fig. 2A). By early 2008 these indicators had attained values only previously observed during the strongest La Niña's of the last few decades. Mixed-layer temperatures off central and southern California responded strongly to these conditions, attaining values similar to those observed during the 1999–2000 La Niña (figs. 10A and 13A). Interestingly, neither SST off Oregon (fig. 6A) nor SST off Baja California responded to these conditions; indeed, unusually high mixed-layer temperatures were observed off Oregon during the summer and off southern Baja

during 2007 (fig. 20). Biological properties of the system showed barely discernable responses; examples are copepod biomass off Oregon (fig. 29), chlorophyll *a* concentrations off Monterey (fig. 10C), and chlorophyll *a* concentrations and zooplankton displacement volumes off southern California (figs. 27A and 32B). This result is surprising since these parameters, with the exception of chlorophyll *a* off southern California, showed a very strong response to the 1999–2000 La Niña conditions. It must be noted that copepod species richness off Oregon changed significantly in 2007 compared to the previous years (fig. 30). However, the change was observed even before La Niña conditions set in, so these changes cannot be unambiguously attributed to La Niña.

Higher trophic levels did not respond systematically to the La Niña conditions in the CCS. The biomass of forage and predatory fish off Oregon and small pelagic fish off California is too variable to attribute any specific change to a single cause. Furthermore, if fish were directly affected by SST, as opposed to system state, these would be expected to respond to the unusually warm conditions off Oregon during the summer. Seabird productivity on the Farallon Islands might have been expected to be affected by the La Niña conditions. However, the timing of the upwelling season is another important factor. The response of seabird productivity during 2007 was mixed. Even though upwelling started early off central California and was strong, seabird productivity for seabirds with conservative life histories showed only modest increases, with the exception of the common murre, which showed a dramatic change. Productivity of seabirds with flexible life histories hardly changed at all compared to the previous two years when productivity was very low.

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Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE, 2007

Hubbs-Sea World Research Institute
San Diego, California
26–28 November 2007

JUMBO SQUID (*DOSIDICUS GIGAS*) INVASIONS IN THE EASTERN PACIFIC OCEAN

Jumbo squid (*Dosidicus gigas*) are an important component of the marine ecosystem and a key target of marine fisheries throughout the Eastern Tropical Pacific (ETP), from the coast of Peru to the Gulf of California. Further north, in the California Current system (CCS), a reappearance of this species off Monterey after the 1997–98 El Niño resulted in an unusual persistence of the new population. Since 2003, jumbo squid have been regularly encountered in large numbers throughout the CCS and as far north as southeast Alaska. Likewise, jumbo squid have recently expanded the southern extent of their range from their traditional distribution along the waters off Peru to the central Chilean coast. In both hemispheres, invasions have been documented throughout the past century, as far back as the 1830s in Chile (Alarcón-Muñoz et al., this volume), however the spatial and temporal extent of the ongoing invasions appear to be unprecedented in the historical record.

Rapidly developing fisheries have landed up to several hundred thousand tons of squid per year in central Chile since 2003, where historical abundance and catches were previously minimal. As a result of this recent increase, and with the continued development of Peruvian, Mexican and high seas fisheries, commercial catches of jumbo squid are now greater than those for any other cephalopod in the world. In 2004 and 2005, nearly 800,000 tons a year were landed, while global annual landings prior to 2000 were never greater than 200,000 tons. Consequently, both the proximate causes of the ongoing range expansion, and the real or potential consequences of the range expansion to marine ecosystems and fisheries, are of major interest to researchers, resource managers and stakeholders throughout the Eastern Pacific Rim. The 2007 Symposium brought together biologists engaged in jumbo squid research from Chile to Canada to address many of these questions; these proceedings represent a substantial subset of that work.

Despite the increasing research efforts into jumbo squid biology, ecology and fisheries, the primary drivers of these range expansions remain uncertain. Climate-related mechanisms appear to be the most plausible, although the remarkable tolerance of adult squid to a wide range of environmental conditions suggests that the effects of climate change are likely to be far more complex than temperature alone. Rodhouse (this volume) provides a comprehensive review of the interactions between climate and ommastrephid squid populations, demonstrating the highly variable boom-and-bust cycles of commercially and ecologically important stocks throughout the Pacific and Atlantic Oceans. In most examples, changes in physical oceanic conditions appear to have played the most significant role, although the potential role of fishing on marine communities has often been invoked as an alternative, or complementary factor (Caddy and Rodhouse 1998; Zeidberg and Robison 2007). Climate change has already been shown to force the range expansions of many marine species towards the poles (Field et al. 2006), with animals with the highest turnover rates showing the most rapid distributional responses to warming (Perry et al. 2005). Jumbo squid would represent an extreme with respect to growth, turnover and adaptability; with the capacity to grow more than 2 mm per day, to nearly 2 m total length in just a little more than a year (Mejía-Rebollo et al., this volume). While the thermal tolerance of jumbo squid might discredit the idea of warming alone as being responsible for range variability and expansion (Gilly et al. 2006), a more subtle climate-related mechanism is certainly plausible.

For example, evidence continues to demonstrate an ongoing expansion of the oxygen minimum zone (OMZ) throughout the ETP, the CCS, and the North Pacific Ocean (Whitney et al. 2007; Bograd et al. 2008; Stramma et al. 2008; Vetter et al. this volume), and projections of

future climate suggest that this response is to be expected under most global change scenarios. A relatively shallow OMZ is a characteristic feature of eastern Pacific ecosystems, particularly in the southeast Pacific Ocean. This reflects the consequences of high levels of upwelling-driven primary production, much of which is metabolized by microbes leading to a vast region of low-oxygen water ranging between 100 to 1000 meters depth (Helly and Levin, 2004). This low-oxygen region provides a refuge for mesopelagic fishes and other organisms from surface-oriented visual predators. Interestingly, jumbo squid have shown a remarkable tolerance for these conditions (Gilly et al. 2006), and are a key predator of mesopelagic organisms in the ETP. In fact, their distribution seems to be linked with the distribution of low oxygen waters in the mesopelagic environment throughout the northeast Pacific Ocean (Gilly and Markaida 2007), suggesting that the ongoing intensification of the OMZ could represent an expansion of favorable habitat.

Potential consequences of these range expansions are difficult to evaluate and quantify. Jumbo squid primarily consume vast quantities of small, mesopelagic organisms, particularly myctophid fishes, in the core of their range (Nigmatullin et al. 2001; Markaida 2006). However, at the periphery in both hemispheres, jumbo squid also forage on commercially and ecologically important fish and invertebrates (Arancibia et al. 2007; Field et al. 2007), including commercially valuable groundfish such as hake (*Merluccius* spp.) and rockfish (*Sebastes* spp.). Yet jumbo squid are also a key forage item for many higher trophic level fishes and marine mammals throughout their range, particularly sperm whales (*Physeter macrocephalus*) and other toothed whales, as well as commercially important tunas, billfish and sharks (Clarke 1976; Olson and Watters 2003; Markaida and Hochberg 2005). The relative contribution of jumbo squid as prey to higher trophic levels can also be tremendous, as emphasized by their relative importance in shortfin mako shark (*Isurus oxyrinchus*) diets off of southern California. Although jumbo squid were rarely encountered in these waters prior to 2002, they comprise 30% to 40% of the diet (by volume) of mako sharks between 2002 and 2006 (Vetter et al., this volume). Similarly, abundance of these key prey items is contemplated as a potential factor in an apparent doubling of the abundance of sperm whales in the California Current over recent years (Barlow and Forney 2007). Consequently, these animals play a major role in structuring the pelagic and mesopelagic ecosystems throughout their range, with a potential mix of both positive and negative impacts to fisheries and fishing communities.

Disentangling the interacting effects of climate, fishing and other ecosystem changes pose considerable challenges in regions where the jumbo squid invasions have taken place. For example, as jumbo squid have become more abundant off of central Chile, the range expansion has been linked with a decline in a key target of Chilean groundfish fisheries, Chilean hake (*Merluccius gayi*). Yet the significance of the contribution of jumbo squid to the decline in hake relative to that of fishing remains the subject of ongoing debate. In fact, Arancibia and Neira (this volume) suggest that the greatest decline in Chilean hake populations took place during a period of high fishing mortality, prior to the onset of high abundance of squid. Their evaluation of the relative impacts of fishing and predation with dynamic ecosystem models indicates that squid predation was negligible relative to the impacts of fisheries and cannibalism. Alternatively, Alarcón-Muñoz et al. (this volume) present an interpretation in which at least part of the decline of hake is attributable to squid. Additionally, as Holmes et al. (this volume) illustrate, the impacts of jumbo squid on fisheries could possibly be more subtle than direct predation alone. Holmes et al. argue that the presence of jumbo squid during hydroacoustic surveys of Pacific hake in the California Current may lead to major changes in hake schooling behavior. Biological consequences of altered schooling behavior are not clear, but impacts on foraging, migrating or spawning would probably be deleterious to a local population. Additionally, altered schooling may confound the ability to monitor, assess, and possibly manage this important commercial resource.

Although there is a growing body of knowledge regarding both the potential causes and likely consequences of jumbo squid invasions, fully understanding the cumulative impacts on marine ecosystems will be difficult. As Markaida et al. (this volume) discuss, jumbo squid appear to show remarkable plasticity in foraging behavior, with a high dependence on mesopelagic micronekton throughout most of their range, coupled with unpredictable horizontal movements that may represent explorations for improved, and opportunistic, foraging grounds. These authors suggest that the balance between stable and opportunistic foraging may be critical in determining how long jumbo squid will remain in a given area, an insight that may prove useful in evaluating the likelihood as well as the consequences of future movement patterns. Similarly, Keyl et al. (this volume) demonstrate that jumbo squid exhibit tremendous plasticity in their rates of growth, maturity and likely survival; key factors that facilitate adaptation to a growing range of marine environments and ecosystems.

All of these points illustrate the tremendous need for a basic science assessment of the life history, distribution and habitat associations, abundance, and ecological impacts of jumbo squid throughout their range. The 2007 Symposium on jumbo squid invasions included eight invited papers, another nine contributed papers, and eight

posters from researchers based in at least seven countries. This reflects the widespread and ongoing efforts throughout the eastern Pacific Ocean to improve our understanding of the life history, distribution, behavior and ecological interactions of these important animals. The articles presented here were refereed by at least two external reviewers and edited by John Heine and Sarah Shoffler, all of whom deserve considerable thanks and credit for their efforts. Additional thanks go to the many symposium presenters and participants, as well as Anne Allen and other SWFSC staff for assisting with logistics. Tremendous thanks are given to the Symposium sponsors, including the Sportfishing Association of California, the California Wetfish Producers Association, the Pacific Marine Conservation Council and the Hubbs SeaWorld Research Institute, whose support was particularly helpful in facilitating widespread international participation.

John Field

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LARGE-SCALE RANGE EXPANSION AND VARIABILITY IN OMMASTREPHID SQUID POPULATIONS: A REVIEW OF ENVIRONMENTAL LINKS

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ABSTRACT

Over the last four decades, several ommastrephid squid stocks have shown rapid expansion and contraction, driving highly variable and sometimes boom and bust fisheries. These include *Illex illecebrosus* in the northwest Atlantic Ocean, *I. argentinus* in the southwest Atlantic Ocean, *Todarodes pacificus* in the northwest Pacific Ocean, *T. sagittatus* in the Norwegian fjords, and *Dosidicus gigas* in the Peru and California Current systems. Explanations for the highly variable behavior of squid populations include: (1) direct effects of environmental variability; (2) changes in prey availability, especially for the early life stages; (3) changes in predation, disease and parasitism; and (4) exploitation of predatory fish which might reduce predation pressure and thus create vacant niches into which the short-lived, ecologically opportunistic squid can expand. This review focuses on the effects of environmental variability on populations and possible interactions with fisheries. Apart from *Dosidicus gigas*, which is associated with the coastal upwelling systems of the Pacific Ocean's eastern boundary currents, the ommastrephid fisheries are mostly pursued in the high energy, western boundary current systems. The environmental variability that will drive changes in population size will differ between these environments. The recent range expansion of *Dosidicus gigas* in the Eastern Pacific Ocean seems to have increased predation pressure on hake stocks off North and South America, which may affect fisheries. The El Niño/Southern Oscillation event in the Pacific Ocean is a well-documented, highly variable oceanographic event and the fisheries along the western seaboard of North and South America are also among the best documented. The *Dosidicus gigas* range expansion over the last decade may provide an opportunity to explore the interacting effects on a squid population of environmental variability and ecological change caused by fishing.

INTRODUCTION

Invasions and range expansions of cephalopod populations have been known to scientists for the best part of at least two hundred years, and may even explain the origin of the late Minoan octopus culture of the eastern Mediterranean Sea around the 15th century B.C., in which images of octopus were used to decorate earthenware from pots and vases to coffins. There are certainly more recent historical records of octopus invasions in the English Channel that caused substantial damage to shellfish fisheries at the turn of the 20th century and again in the 1950s (Garstang 1900; Rees and Lumby 1954).

In the Eastern Pacific Ocean, D'Orbigny (1835–43) describes large strandings of *Dosidicus gigas* on the Chilean coast in the early 19th century, and there are also reports of the species being very abundant off the west coasts of North and South America in the 1930s (Clark and Phillips 1936; Gunther 1936; Croker 1937). Over the last decade, and since the major 1997 El Niño/Southern Oscillation (ENSO) event, there has been a large-scale range expansion of *Dosidicus gigas* northwards as far as Alaska and southwards to southern Chile (Field et al. 2007; Zeidberg and Robison 2007). The cause of this expansion is debated, and ranges from the relative importance of life history response to thermal change and the possible effects of the reduction of tuna stocks from overfishing (e.g., Watters et al. 2008; Zeidberg and Robison 2008). Compounding this debate are the changes in the structure of the pelagic community off both North and South America. Holmes et al. (2008) suggest that the range expansion of *Dosidicus gigas* has increased predation pressure of squid on hake stocks off North and South America, which may have caused changes in hake behavior. This may also have implications for the hake fisheries (Arancibia and Neira 2008).

Elsewhere, fishery data records have quantified the magnitude of variability of population size of exploited cephalopod species, especially of the family ommastrephidae. The longest record exists for the Japanese *Todarodes pacificus* fishery in the Kuroshio/Oyashio current system, for which data go back to the beginning of the 20th century. These data indicate that the population size varied on both an annual and a decadal basis, with higher catches during warm phases in the decadal record of the local climate regime (Sakurai et al. 2000) (fig. 1). A shorter data set exists for *Illex argentinus* in the southwest Atlantic Falkland/Brazil Current system, where the catches varied interannually by over an order of mag-

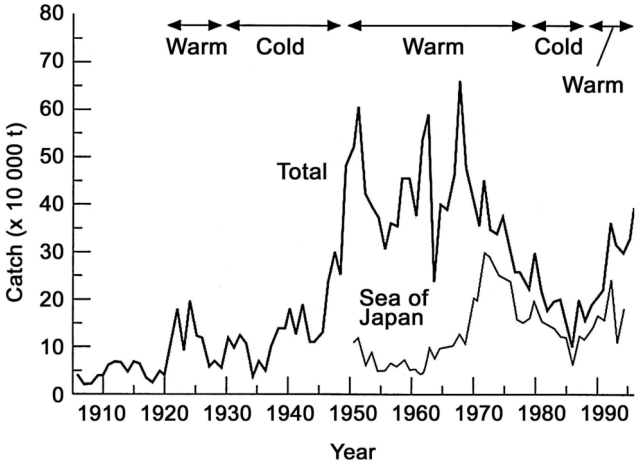

Figure 1. Annual variability in the total Japanese catch of *Todarodes pacificus* in the northwest Pacific Ocean and in the Sea of Japan (source: Sakurai et al. 2000).

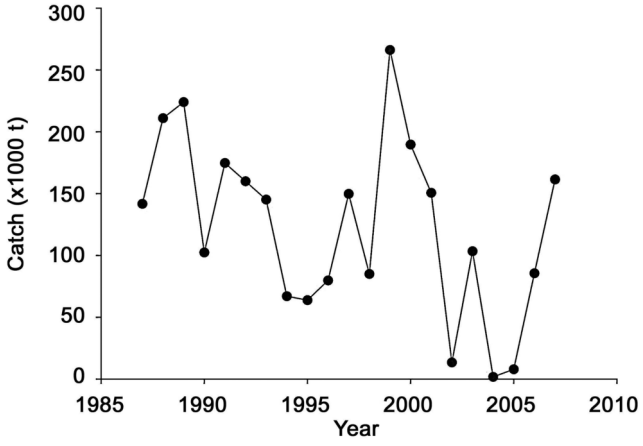

Figure 2. Annual variability in the catch of *Illex argentinus* in the Falkland Islands fishery, southwest Atlantic Ocean (source: Falkland Islands Government Fisheries Department Statistics, Stanley, Falkland Islands).

nitude in two decades (fig. 2). Similarly, a short-term data set for *I. illecebrosus* in the northwest Atlantic Gulf Stream/Labrador Current system illustrates the short boom-and-bust cycle of that fishery in the decade 1973–83 (fig. 3). The Peruvian fishery for *Dosidicus gigas* has been very well documented since the inception of an industrial fishery in the early 1990s; the record includes the period of the extreme ENSO event of 1997–98 and shows a dramatic variability in abundance since the beginning of the record (fig. 4).

These fisheries all use lights and jigs and are visible in Defense Meteorological Satellite Program (DMSP) imagery (Rodhouse et al. 2001). These images have been used to follow the spatial dynamics of the fisheries (Kiyofujo and Saitoh 2004; Waluda et al. 2002; 2004; 2005), and in a recent paper, Waluda et al. (2008) related interannual changes in catch of *Illex argentinus* to changes in the distribution of the fishing fleet.

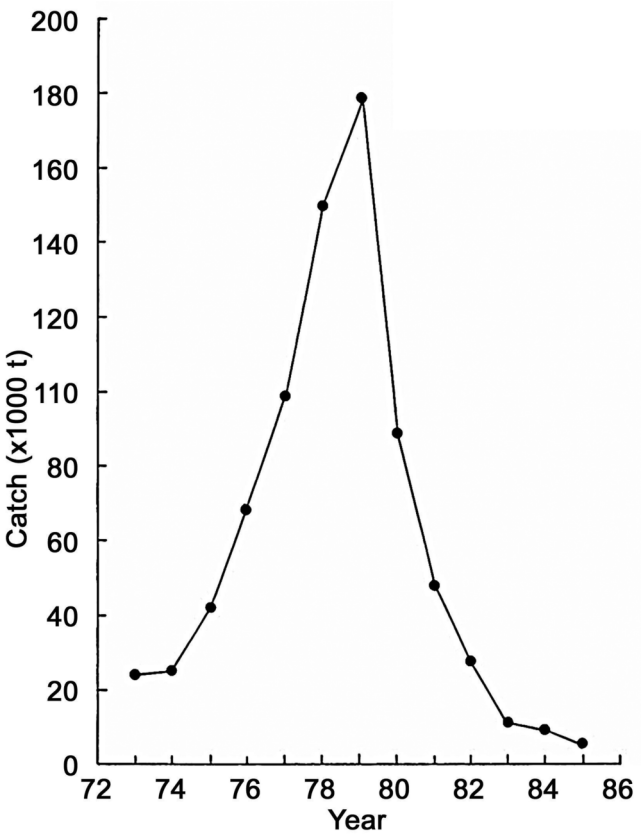

Figure 3. Annual variability in the catch of *Illex illecebrosus* in the northwest Atlantic Ocean (source: FAO Fishery Statistics, FAO, Rome).

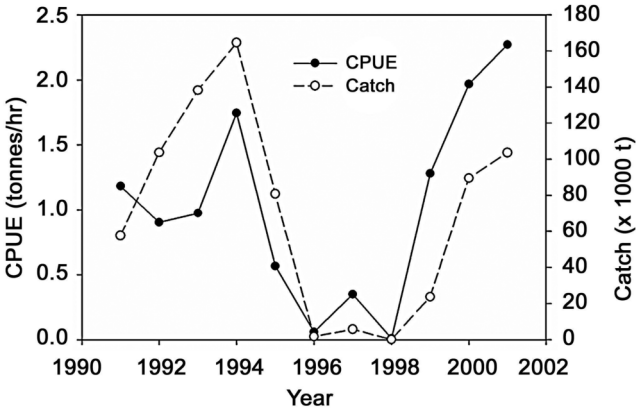

Figure 4. Annual variability in catch and catch per unit effort (CPUE) for jumbo squid, *Dosidicus gigas,* in Peruvian waters (source: Instituto de Mar del Perú, IMARPE, Callao, Peru).

The purpose of this paper is to review the theoretical causes of variability in size and range of ommastrephid squid populations and to examine the data in order to test some of the theoretical causes. Given the scale of the processes involved, data from the commercial fisheries provide insight into population processes and remotely sensed oceanographic data provide a better understanding of the environmental processes. The possible interaction of fishery effects on the ecosystems inhabited by

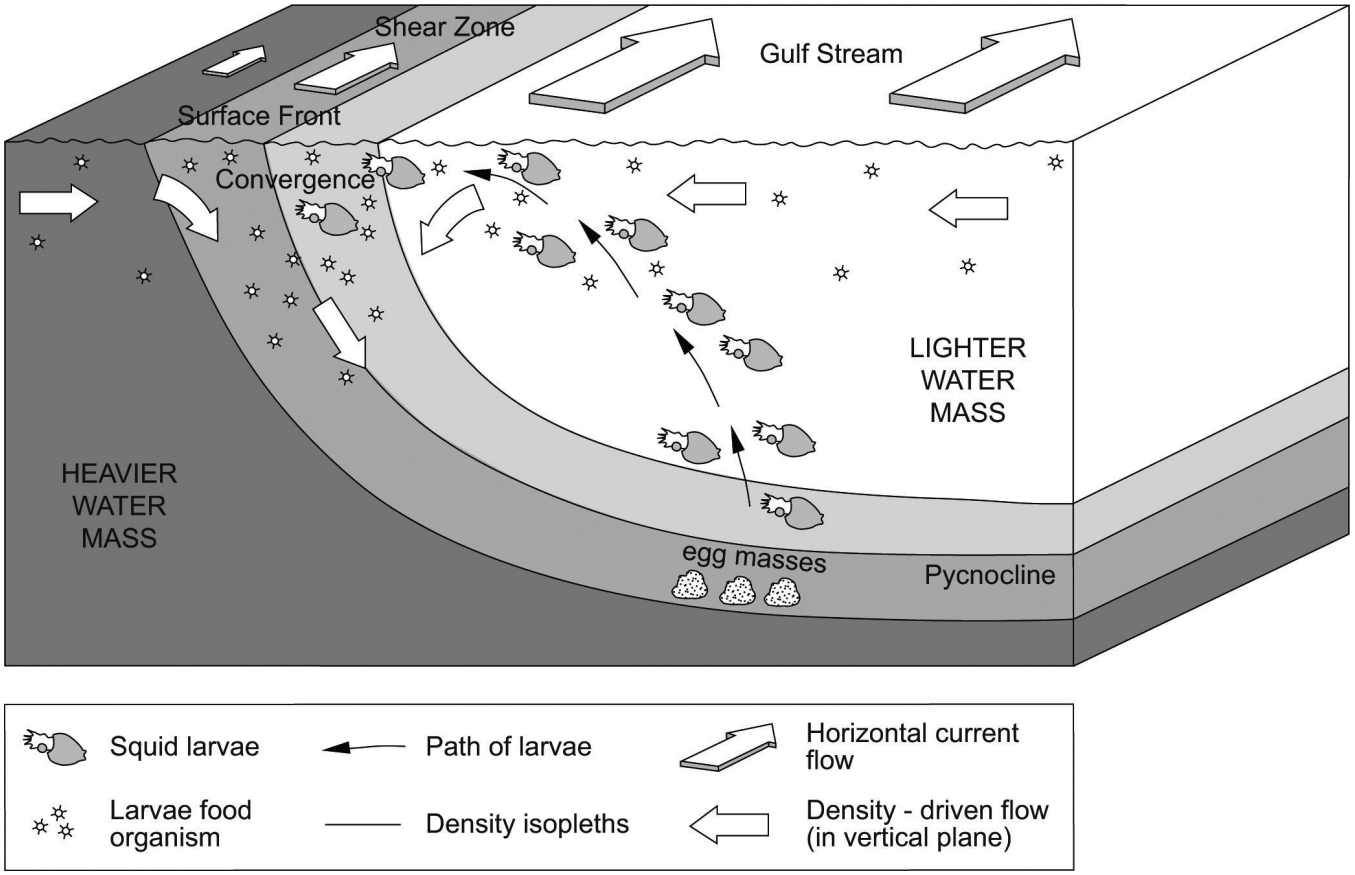

Figure 5. Schematic diagram showing the relationship between the early life cycle of an ommastrephid squid and the physical oceanographic processes at the convergent frontal zone between the waters of a western boundary current (e.g., the Gulf Stream) and adjacent shelf slope water (source: Bakun and Csirke 1998).

ommastrephid squid and environmental variability is also considered, as this may be one of the multiple causes of variability and change in these squid populations.

BIOPHYSICAL INTERACTIONS—THEORETICAL CONSIDERATIONS

The body of theory that explains and predicts variability in cephalopod populations in relation to fisheries has largely focused on interactions between biological processes, especially in the early life stages of eggs and paralarvae, and physical oceanographic variability.

Western-boundary current systems

Most of the large fisheries for ommastrephid squid occur in the western-boundary current systems of the northwest Pacific Ocean (*Todarodes pacificus*), the southwest Atlantic Ocean (*Illex argentinus*), the northwest Atlantic Ocean (*Illex illecebrosus*), and the southwest Pacific Ocean (*Nototodarus gouldi* and *N. sloanii*). These currents are powerful, meandering systems that generate warm- and cold-core rings and provide "rapid transport" systems for planktonic squid eggs and larvae.

Understandably, in view of the importance of fisheries in these systems, most theory and data on the interactions between squid populations and physical oceanography have been focused on the stocks inhabiting western-boundary current environments. The ommastrephid life cycle in these systems is generally well known (Okutani 1983; Haimovici 1998; O'Dor and Dawe 1998). The squid have a one-year life span and spawn in low-latitude warm water. The planktonic eggs and larvae develop in this environment and are subject to transport by ocean currents. When the juvenile squid have grown into the nektonic phase, some, or all, of the young population migrates in the direction of the prevailing flow into cooler, higher latitude waters where productivity is higher, food is more abundant, growth is faster, maximum size is larger, and hence, fecundity is maximized (O'Dor and Coelho 1993).

A theoretical framework for recruitment variability in western-boundary current ommastrephid squid populations has been set out by Bakun and Csirke (1998). They identify the habitat requirements for squid reproduction to be: (1) food web enrichment by physical processes, e.g., upwelling; (2) a mechanism for formation of concentrated patches of food such as convergent

flow patterns and frontal systems; and (3) flow mechanisms that allow the population to maintain itself. Bakun and Csirke (1998) propose that western boundary currents meet these habitat requirements (fig 5).

Fast-flowing geostrophic currents, for example, the Gulf Stream and the Brazil and Kuroshio Currents, occur at the interface of waters of different density (i.e., shelf/slope waters and offshore waters of the oceanic gyre) where baroclinic pressure balances Coriolis accelerations generated in high-speed ocean currents. When the two water masses of different density and relative motion come together, dynamic forces generate flow convergence towards the intersection and friction in the shear zone perturbs geostrophic balance. Gravity and pressure cause the denser shelf/slope water to sink below the less dense oceanic water, which then overflows the shelf/slope water. Mixing at the interface produces water of intermediate density which flows below the surface water. Both the high- and low-density water masses thus form a mass of mixed water that sinks at the interface. The buoyancy-driven flows that supply the formation of this mixed water are directed from each water mass towards the interface, resulting in a convergence zone that sustains the frontal boundary.

Bakun and Csirke (1998) describe these processes: these processes form a pycnocline (see fig. 5) where ommastrephid egg balloons are neutrally buoyant at a depth where there are suitable temperatures and low predation. The hatching paralarvae rise to the surface and are carried to the convergent frontal zone by the density-driven flow described above. In the frontal zone, eddy formation drives upwelling of nutrient-rich water which enriches the food chain. Furthermore, convergence at the surface front and in its meanders concentrates the food resource.

In addition to the above processes, western-boundary current systems potentially provide rapid transport of eggs and paralarvae from the spawning ground to the feeding ground. However, this might be reduced in the frontal shear zone between the boundary current and shelf water, and the distance carried will be increased in meanders that will lengthen the trajectory. Warm-core eddies will carry eggs and paralarvae onto the continental shelf providing a positive advantage. Conversely, cold-core eddies will carry eggs and paralarvae into the ocean interior where they will be lost from the population.

Hypotheses concerning recruitment variability in relation to physical oceanographic variability assume that favorable conditions exist when: (1) the surface frontal zone maintains its integrity and there is a low frequency of core ring formation; (2) eggs and paralarvae are transported from the oceanic gyre to the shelf adult feeding grounds; (3) food availability and low predation favor adult counter migration; (4) paralarva hatch when in the presence of food; and (5) there are low levels of predation, disease, and parasitism throughout the life cycle.

Eastern-boundary current systems

Large populations of *Dosidicus gigas* inhabit the eastern-boundary current systems of the eastern Pacific Ocean and support important fisheries in the Peru Current upwelling system in the southeast Pacific Ocean and in the Gulf of California. Eastern-boundary currents provide a different environment to western-boundary currents; they are weak and characterized by regions of major coastal upwelling that support high primary productivity which, in turn, provides squid populations with enriched feeding conditions. The theory concerning which factors drive recruitment variability is less well developed for the eastern-boundary current systems. However, the interactions between ENSO events and production processes in the eastern Pacific coastal upwelling systems are well known and appear to play a major part in driving variability in *Dosidicus gigas* recruitment and population size (Waluda et al. 2006; Yamashiro et al. In prep.). By relaxing the flow of surface water from the coast into the interior of the Pacific Ocean, ENSO events may favor retention of eggs and paralarvae in the nearshore regions where the fishery is pursued (Anderson and Rodhouse 2001). Conversely, during normal conditions and cold (La Niña) events, offshore transport of surface water may cause entrainment of eggs and paralarvae towards the central Pacific Ocean so that they are dispersed and the cohort develops over a larger area at a lower density.

BIOPHYSICAL INTERACTIONS—OBSERVATIONAL DATA

Western-boundary current systems

The influence of environmental variability on ommastrephid squid population size and extent has been analyzed using Japanese catch data and paralarval densities for *Todarodes pacificus* together with remotely sensed sea surface temperature (SST) data (Sakurai et al. 2000). Egg and paralarvae data suggest that the spawning grounds occur over the continental shelf at sea surface temperatures between 15°–23°C. Using SST data analyzed with GIS technology, it was shown that since the late 1980s, winter spawning areas over the continental shelf and slope in the East China Sea (defined by 15°–23°C) have expanded over the distribution range of the population and separate autumn and winter spawning areas have coalesced. This has been coincident with increases in abundance reflected by catch rates (catch per unit effort or CPUE) of adult *T. pacificus* (fig. 1) and paralarval densities. The conclusion to be drawn here is that as the available thermal habitat suitable for spawning and egg and

paralarval survival increases, the population has responded positively and population size has increased.

In the southwest Atlantic Ocean, a similar approach combining data from the *Illex argentinus* fishery and remotely-sensed SST data was taken (Waluda et al. 1999). An analysis of SST on the spawning grounds around the Patagonian shelf edge at 35°S and CPUE in the Falkland Island fishery the following fishing season—when the progeny from the spawning ground would be exploited—was carried out over a thirteen-year period. It was found that adult abundance was influenced by SST on the spawning grounds in the winter spawning season prior to the fishery. The relationship was negative and SST on the spawning grounds explained about 45% of the variability in population size over the time covered by the study. Time-series analysis revealed that there were connections between SST in the south Atlantic Ocean and ENSO events in the tropical Pacific Ocean, with a two-and-a-half year lag between the Pacific Ocean and the southern Patagonian shelf (where the fishery is pursued), and a five-year lag between the Pacific Ocean and the northern Patagonian shelf (where the spawning grounds are located). This suggests that population variability in the *Illex argentinus* population in the south Atlantic Ocean is ultimately driven by ENSO events in the Pacific Ocean.

In a further study, Waluda et al. (2001) examined the possible influence of mesoscale oceanographic variability in the spawning area on subsequent recruitment success in the *Illex argentinus* fishery. The study had two parts: the first examined the relationship between recruitment in the Falkland Islands fishery and the integrity of the confluence front in the spawning area around the Patagonian shelf edge at 35°S; and the second part examined the relationship between recruitment and the proportion of the spawning area in which the surface water ranged from 16°–18°C, *I. argentinus'* preferred temperature range (Brunetti and Ivanovic 1992). The results showed that higher abundance in the fishery was associated with a lower percent area of confluence front waters in the spawning ground during the spawning season prior to recruitment. This explained about 51% of the variance in abundance. Higher abundance was also associated with a higher percent area occupied by 16°–18°C SST waters on the spawning ground during the spawning season prior to recruitment. This explained about 55% of the variance in abundance. The study suggests that when the confluence front is weak, eggs and paralarvae are retained/transported in the spawning area close to the shelf and that, in common with Sakurai et al.'s (2000) conclusion, recruitment is higher with increased availability of suitable SST habitat.

Dawe et al. (2000), using a seventy-three-year time series of catch and meteorological data illustrated that environmental variability drives *Illex illecebrosus* recruitment. Abundance was positively related to the negative phase of the North Atlantic Oscillation, high water temperature, and southward shifts in the Gulf Stream and the boundary between shelf and offshore slope water. Increased meandering in the Gulf Stream was associated with increased abundance, consistent with observations by Waluda et al. (2001).

Dawe et al.'s (2007) analysis of ocean climate effects on the relative abundance of the squids *I. illecebrosus* and *Loligo pealeii* in the northwest Atlantic Ocean suggests that the efficiency of downstream dispersal of the highly migratory *I. illecebrosus* by the Gulf Stream and the survival of young stages are affected by variation in the latitudinal position of the shelf/slope front. *L. pealeii* population size, however, is favored by higher inshore water temperatures, which explains the range expansion of *L. pealeii* in the year 2000.

Eastern-boundary current systems

The only major fisheries for an ommastrephid squid in an eastern-boundary current system are those for *Dosidicus gigas* in the Eastern Pacific Ocean, and these are pursued off the coast of Peru and in the Gulf of California. Whilst there has been less research effort to understand processes driving variability of squid stocks in the eastern-boundary current systems, this species clearly shows cyclical changes in population size, reflected in fishery catch and catch rates, in relation to the sequence of ENSO events since the early 1990s (Waluda et al. In press; Yamashiro et al. In prep.).

One of the difficulties with understanding *Dosidicus gigas* variability is that its life cycle is less well known than are those of *Illex* spp. and *Todarodes pacificus*. Nevertheless, Waluda and Rodhouse (2006) analyzed interactions between physical conditions on the putative *D. gigas* spawning grounds and abundance in the fishery in the following fishing season. The analysis used Ichii et al.'s (2002) data on the optimum temperature for *D. gigas* hatching (24°–28°C) and assumed that at least one major spawning ground for the species lies in the region of the Costa Rica Dome (Wyrtki 1969), where Vecchione (1999) found large numbers of ommastrephid paralarvae. There was correlation between CPUE in the Peruvian fishery and the proportion of the putative spawning grounds occupied by optimum sea surface temperatures in September, which is when hatching of squid that recruit to the Peru fishery has been shown to occur (Tafur et al. 2001).

ECOLOGICAL CHANGE IN GLOBAL FISHERIES

The effects of ecological change driven by overexploitation of fishery resources, especially groundfish stocks, on changes in size and geographic range of cephalopod populations have also been considered. Caddy

and Rodhouse (1998) showed that as global groundfish landings decreased over the last three decades of the 20th century, cephalopod landings increased. More specifically, in all but one of fifteen FAO areas, cephalopod landings increased over this time while groundfish landings rose slowly, stabilized, or declined. Cephalopod biomass has not completely replaced fish biomass in the landings, possibly because cephalopod biomass turnover is higher due to a shorter life. The underlying concept is that under intense fishing pressure, groundfish such as hake are likely to be poor competitors with cephalopods which have high growth and reproductive rates, short life cycles, high feeding rates, and voracious predatory habits.

Large-scale range expansion and variability in size of cephalopod populations may have a number of causes, some of which may be natural and/or anthropogenic ocean climate variability and change as well as large-scale ecological change driven by overexploitation of other fish stocks.

DISCUSSION

The recent range expansion of *Dosidicus gigas* in the eastern Pacific Ocean is exceptional and appears to have been triggered by the major ENSO event in 1997–98. Long-lasting physical changes appear to have been triggered by the same event resulting in, among other things, mass shifts of water in the southern Pacific and Indian Oceans at a magnitude sufficient enough for changes in the earth's shape to be detectable by satellite (Dickey et al. 2002). To determine if and how the many oceanic physical, chemical, and biological changes associated with ENSO have influenced the changes in squid stocks will require more sophisticated analyses than have been described in this short review. In most analyses, the physical factors that have been examined explain less than 50% of the variability in squid landings. There is evidence of synchronicity in the abundance of three southern Pacific squid stocks (Waluda et al. 2004). These are all associated with major current systems that are connected to the Antarctic Circumpolar Current. Further, variability in abundance has been found to be correlated with the Southern Oscillation and the Trans Polar Index, so common factors do seem to be involved. Future research will benefit from developing the concept of biological processes, such as range expansion and population explosions, as emergent properties of highly complex systems. The developing field of complexity theory may have much to offer ecologists in this regard. And to understand the processes that drive regime shifts in ocean ecosystems requires at least an understanding of the interactions between change and variability in the ocean climate system and fisheries (Scheffer et al. 2001).

The ENSO system in the Pacific Ocean is one of the better understood variable ocean climate systems in the world. The fisheries along the western seaboard of North and South America are among the best documented. Therefore, the recent *Dosidicus gigas* range expansion and associated changes in the pelagic ecosystem over a very large area provide an opportunity to explore the interacting effects of environmental variability and change as well as ecological change caused by fishing.

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FOOD AND FEEDING OF JUMBO SQUID *DOSIDICUS GIGAS* IN THE CENTRAL GULF OF CALIFORNIA DURING 2005–2007

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ABSTRACT

Stomach contents were analyzed for 249 jumbo squid (*Dosidicus gigas*) of 35–80 cm mantle length. All squid were sampled in the central Gulf of California in 2005–07, primarily on the commercial fishing grounds of Santa Rosalia during different times of the year. Diet off Santa Rosalia was mainly composed of mesopelagic micronektonic organisms, mostly the myctophids *Benthosema panamense*, *Triphoturus mexicanus*, and the squid *Pterygioteuthis giardi*. Pteropods and crustaceans made up a smaller portion of the diet. Squid sampled elsewhere revealed that the pelagic red crab, *Pleuroncodes planipes*, and northern anchovy, *Engraulis mordax*, could also be major dietary items. Cannibalism incidence increased with squid mantle length. We propose that the main prey of jumbo squid in the central Gulf of California derives from the mesopelagic community associated with the upper boundary of the oxygen minimum layer, a well-developed midwater feature in this region. In addition, opportunistic foraging on a variety of organisms supplements their dietary intake. These data are discussed in conjunction with recent electronic tagging data that revealed vertical and horizontal movements of jumbo squid. This work demonstrates a need to study the dynamics of the oxygen minimum layer and the composition of the deep-scattering layer over the upper slope of Guaymas basin.

INTRODUCTION

The first phase of commercial fishing for jumbo squid, *Dosidicus gigas*, in the Gulf of California began in 1974 and ended in 1981 (Ehrhardt et al. 1983). The fishery collapsed during and after the strong 1982–83 El Niño. Up to that time, stomach content analysis showed that jumbo squid from the Gulf fed mainly on neritic and small pelagic fishes (sardines, mackerels), pelagic red crab, and myctophids, with cannibalism also occurring (García-Domínguez and González-Ramírez 1988, Ehrhardt 1991). Ehrhardt (1991) therefore suggested that jumbo squid may have effects on the important commercial sardine resource. This paper is arguably the most historically influential study of *Dosidicus* diet, and the conclusion of sardine predation has been widely cited in reviews on cephalopod feeding (see Boyle and Rodhouse, 2005).

A largely artisanal fishery resumed in 1994 for a form of *D. gigas* that matures at a large size (40–85 cm mantle length, ML), operating close to shore in the Guaymas Basin, both in the States of Sonora and Baja California Sur. Annual landings were over 100,000 tonnes in 1995–97. During this period most squid were taken off Santa Rosalia, Baja California, between May and November, and the remaining off Guaymas, Sonora, between December and April (Markaida and Sosa-Nishizaki 2001). In contrast to results of earlier studies, Markaida and Sosa-Nishizaki (2003) found that these large squid fed mostly on mesopelagic micronekton, mainly myctophids.

The squid fishery in the central Gulf collapsed again in 1998 following the 1997–98 El Niño. Smaller squid that matured at <45 cm ML re-established the fishery in the following year after a transition to La Niña conditions. These smaller squid again fed mostly on myctophids (Markaida 2006). Since 2000, large squid have again dominated the fishery in the central Gulf (Nevárez-Martínez et al. 2006; Bazzino et al. 2007), but dietary studies have not been reported during this period.

This paper presents an analysis of jumbo squid feeding in the central Gulf of California during the period of 2005–07 based on samples made on the commercial fishing grounds off Santa Rosalia during different times of the year and on samples opportunistically collected from elsewhere in the Gulf. Diet was mainly composed of mesopelagic micronekton, primarily myctophid fishes. Although opportunistic foraging on anchovies and other small fishes does occur, no evidence of sardine predation was found.

Recently (since 2002), *Dosidicus gigas* has undergone a major northern range expansion to as far north as southeast Alaska (Wing 2006). Because *Dosidicus gigas* is an abundant and highly migratory predator, shifts in diet

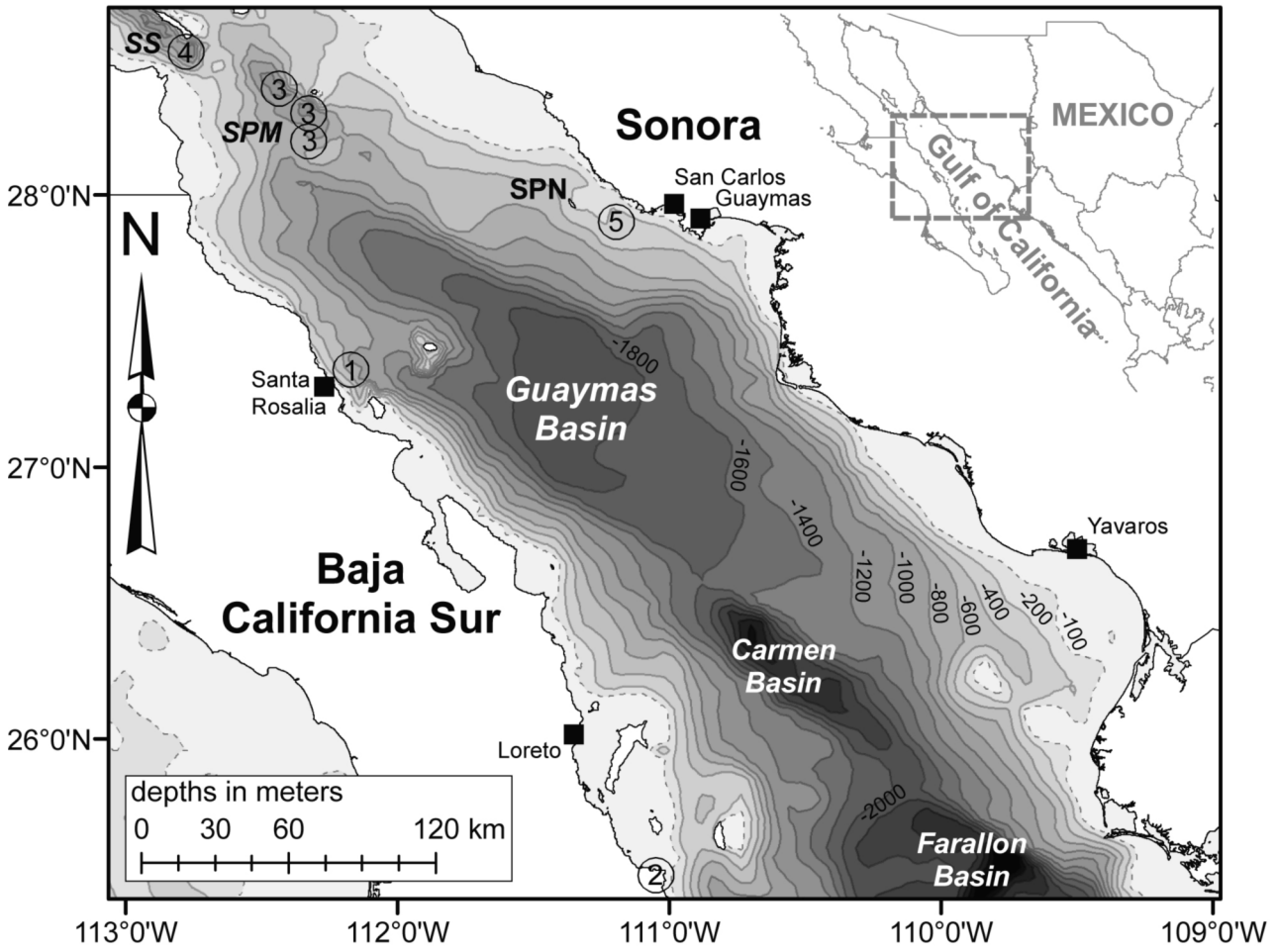

Figure 1. Central Gulf of California showing locations (as listed in Table 1) where samples were taken by number and name as used in text: 1 - Santa Rosalia; 2 - Point San Marcial; 3 - San Pedro Martir Basin (SPM); 4 - Salsipuedes Basin (SS); and 5 - San Carlos. Basin names are in italics. SPN is San Pedro Nolasco Island. Depths are in meters.

likely have important ecological implications, including possible impacts to commercially important groundfish stocks. Thus, it is important to compare dietary content of squid in the core location of the central Gulf to that in newly invaded areas to the north. Stomach contents from squid sampled in the Pacific Ocean, both off the Baja peninsula in Mexico (Bazzino et al., submitted) and off northern California (Field et al. 2007), clearly show that *Dosidicus* forages not only on micronekton, but also on a variety of neritic resources, including hake and, in the California case, sardines. The goal of this study was to monitor dietary changes in association with temporal and spatial changes in abundance of this opportunistic predator.

MATERIALS AND METHODS

Jumbo squid were collected by jigging, generally after dusk, in the central Gulf of California during 2005–07 (see fig. 1). Stomachs of 249 squid from nine samples (a group of stomachs, collected at a given locality and date) were analyzed. These included five samples collected on the Santa Rosalia fishing grounds at various times of the year between June 2005 and November 2007. Samples were also collected from the northern basins of San Pedro Martir and Salsipuedes in July 2006 and from San Carlos, Sonora, in March 2007. Another sample was obtained from animals discovered in the intertidal after a stranding at Point San Marcial, Baja California Sur, in May 2006. Sample size ranged from 10 to 57 stomachs (tab. 1). The dorsal ML (to the nearest mm) was measured in all squid except for the Point San Marcial sample (these squid were in the 25–30 cm ML range) and for 16 animals from San Pedro Martir basin. Sex and stage of maturity were assigned according to Lipiński and Underhill (1995). All squid analyzed in this study belong to the form of *Dosidicus gigas* that matures at large body size, with mature females ranging 40–82 cm ML and mature males 41–74 cm ML (see fig. 2).

Stomachs were kept frozen at –20°C until analysis in the laboratory. A subjective, visual stomach fullness index

TABLE 1
Summary data for jumbo squid (*Dosidicus gigas*) collected for stomach contents analysis in the Gulf of California during 2005–07.

Location	Date	Sex			Total	ML[a] (cm)
		Females	Males	Unknown		
Santa Rosalía	13 Jun 2005	16	13	1	30	41–67
	6–14 Jul 2006	19	7		26	49–72
	20 Oct 2006	11	3		14	66–82
	22 Mar 2007	22	15		37	41–74
	10 Nov 2007	19	14		33	46–73
Point San Marcial[b]	17 May 2006			22	22	25–30
San Pedro Mártir	17, 20, 21 Jul 2006	35	6	16	57	25–81
Salsipuedes Basin	18 Jul 2006	14	4	2	20	44–73
San Carlos	13, 18 Mar 2007	9	1		10	38–70
Total		145	63	41	249	25–82

[a]ML, mantle length
[b]Stranded individuals

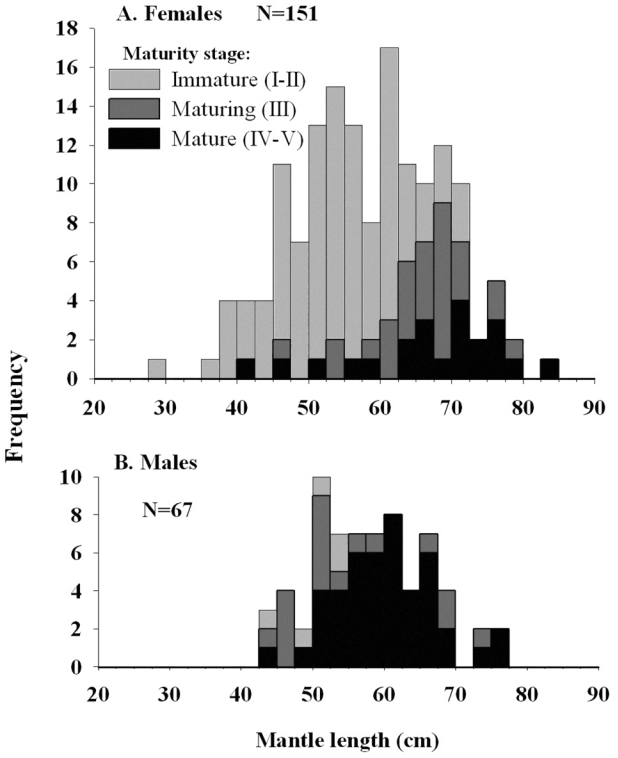

Figure 2. Distribution of ML and sexual maturity state for female (A) and male (B) jumbo squid (*Dosidicus gigas*) collected in the central Gulf of California for stomach content analysis.

(FI) was assigned: 0, empty; 1, scarce remains; 2, half full; 3, almost full; and 4, completely full (Breiby and Jobling 1985). In order to preserve hard remains of prey for identification, stomach contents were screened through a 0.5 mm mesh sieve with gentle washing. The screened contents were observed under a binocular dissection microscope (60–120×) over both a black and a white background to aid recognition. The advanced degree of digestion of stomach contents generally impedes exact and complete separation of prey for weighing (Breiby and Jobling 1985). For this reason, only the most conspicuous prey items were weighed to the nearest 0.1 g.

Identification of fish sagittal otoliths was made by consulting available keys (Fitch and Brownell 1968; Fitch 1969a, b; Harvey et al. 2000; García-Godos Naveda 2001; Mascareñas-Osorio et al. 2003). Cephalopod beaks were identified following Clarke (1986). Reference collections held at Laboratorio de Pesquerías Artesanales at ECOSUR Unidad Campeche were also used to identify otoliths and squid beaks. Undigested pieces of squid flesh, indicative of cannibalism, were considered apart from other prey (see Markaida and Sosa-Nishizaki 2003). Pelagic gastropods were identified after McGowan (1968). Crustaceans were identified by their exoskeleton. The number of fish or cephalopods consumed was estimated as the maximum number of right or left fish otoliths, or of upper or lower cephalopod beaks (Antonelis et al. 1984). When prey lenses were more numerous than otoliths or beaks, they were counted as fish lens pairs or as the maximum number of proximal or distal sections of cephalopod lenses, divided by two.

Frequency of occurrence, numeric, and gravimetric (volumetric) methods were used to quantify diet. Frequency of occurrence (%FO) was calculated as the percentage of stomachs in which the prey occurs in any given sample. Number (%N) is the percentage of stomachs in which the prey occurs relative to the total number of stomachs, and weight (%W) is defined as the wet weight of a certain prey type relative to the total wet weight of all prey. %N and %W were calculated from data pooled from all stomach contents in a given sample and expressed as percentages (Cailliet 1977). Graphs of the index of relative importance, IRI = (%N + %W) × (%FO) were plotted to illustrate monthly diet composition following Pinkas et al. (1971). Only prey species or taxa with IRI values >1% were included in this analysis.

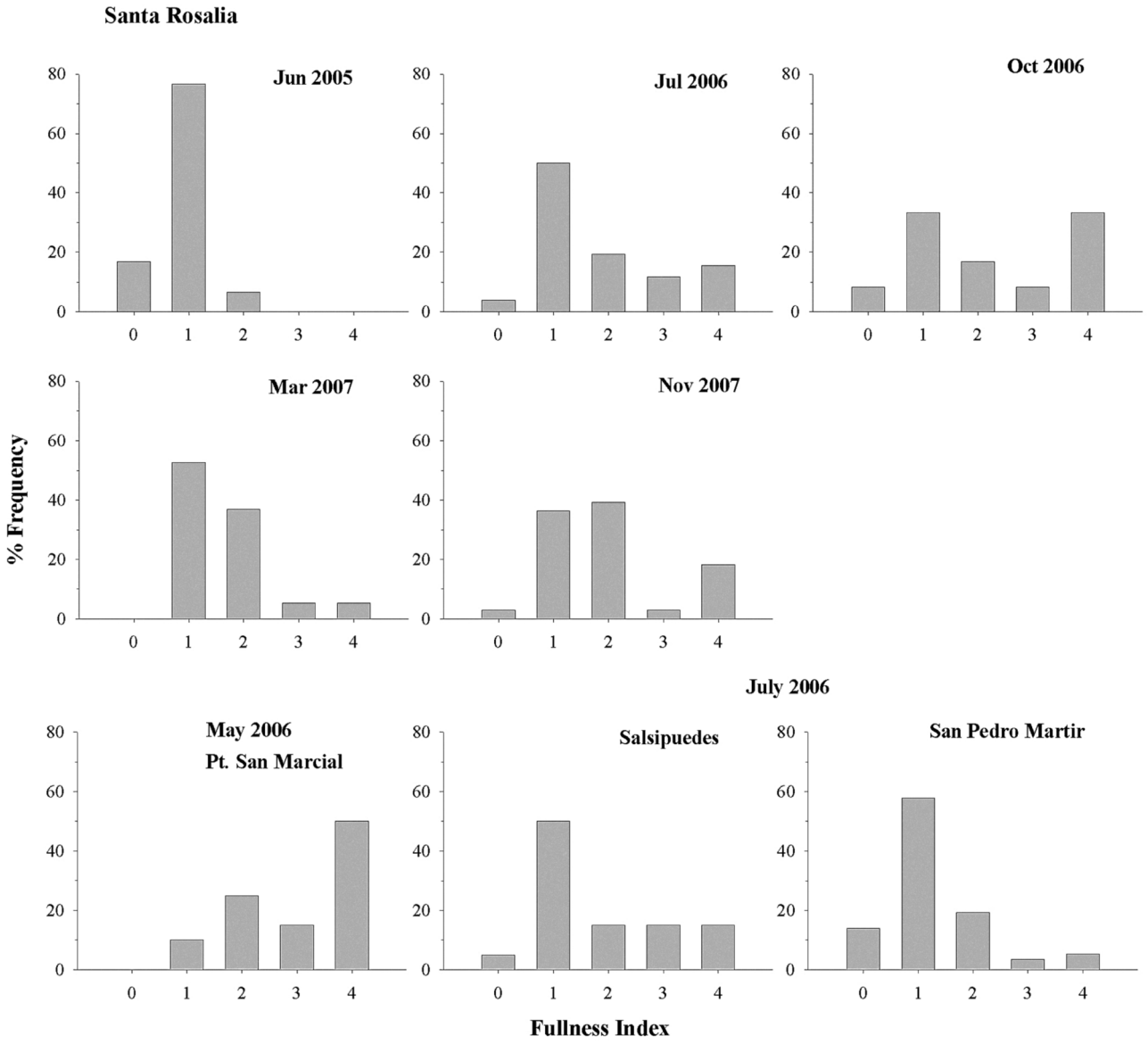

Figure 3. Frequency of occurrence for the range of stomach fullness indices across localities and seasons in the central Gulf of California during 2005–07.

The lengths of up to 15 of the best preserved otoliths of each fish species per stomach were measured to the nearest 0.1 mm. The size of ingested fish was calculated from the otoliths using relationships for each species or genus (Aurioles-Gamboa 1991; Harvey et al. 2000; Markaida and Sosa-Nishizaki 2003). The relationships between total length (TL, mm), standard length (SL, mm), body weight (BW, g), and otolith length (OL, mm) for a sample of *Triphoturus mexicanus* we collected in the central Gulf were calculated as follows:

$$TL = 15.0324 + 39.4418\ OL \quad r^2 = 0.71 \quad n = 81$$

$$SL = 14.0445 + 28.5722\ OL \quad r^2 = 0.60 \quad n = 101$$

$$BW = 0.6437 \times OL^{2.1481} \quad r^2 = 0.53 \quad n = 101$$

Lower rostral lengths (LRL) of squid beaks were measured to the nearest 0.1 mm. Upper beak dimensions were used in the absence of lower beaks. Ingested squid ML and BW were estimated using the relationships provided by Clarke (1986) and Wolff (1984). Relative prey size was calculated as the percentage of estimated prey size (TL or ML) relative to jumbo squid ML. Correlation between relative prey size and squid size was tested for the most numerous prey species.

RESULTS

Stomach Fullness

The stomach fullness index was observed for 218 squid (fig. 3). They were not recorded for 27 stomachs taken

TABLE 2
Frequency of occurrence (FO), number, and weight of prey in the stomach contents of 249 jumbo squid (*Dosidicus gigas*) from the Gulf of California during 2005–07.

	FO		Number		Weight	
Prey	FO	FO%	N	N%	g	W%
PISCES	129	51.8	530	44.0	271.9	9.5
Myctophidae:	77	30.9	380	31.5	87.2	3.0
Benthosema panamense	56	22.5	206	17.1	74.6	2.6
Triphoturus mexicanus	23	9.2	153	12.7	0.0	0.0
Diogenichthys laternatus	9	3.6	11	0.9	0.0	0.0
Unidentified Myctophidae	10	4.0	10	0.8	12.6	0.4
Photichthydae:						
Vinciguerria lucetia	6	2.4	8	0.7		
Engraulidae:						
Engraulis mordax	32	12.9	86	7.1	109.0	3.8
Merlucciidae						
Merluccius angustimanus	3	1.2	3	0.2		
Batrachoididae:						
Porichthys sp.	2	0.8	2	0.2		
Carangidae:						
Trachurus symmetricus	1	0.4	1	0.1	3.2	0.1
Scombridae:						
Scomber japonicus	3	1.2	3	0.2	9.4	0.3
Argentinidae:						
Argentina sialis	1	0.4	1	0.1		
Unidentified Teleostei	30	12.0	46	3.8	63.1	2.2
CEPHALOPODA	79	31.7	459	38.1	5.4	0.2
Pyroteuthidae:						
Pterygioteuthis giardi	55	22.1	333	27.6	2.1	0.1
Gonatidae:						
Gonatus sp.	10	4.0	11	0.9		
Enoploteuthidae:						
Abraliopsis affinis	7	2.8	10	0.8		
Octopoda:						
Octopus sp.	1	0.4	1	0.1		
Unidentified Cephalopoda	26	10.4	104	8.6	3.3	0.1
PTEROPODA						
Unidentified Thecosomata	14	5.6	71	5.9		
CRUSTACEA	20	8.0	44	3.7	136.0	4.7
Euphausiacea	1	0.4	1	0.1		
Isopoda	1	0.4	1	0.1		
Copepoda	1	0.4	6	0.5		
Unidentified Decapoda	1	0.4	1	0.1	22.4	0.8
Pleuroncodes planipes	14	5.6	32	2.7	113.6	4.0
Brachiura	3	1.2	3	0.2		
Unidentified Crustacea	12	4.8	17	1.4	6.9	0.2
Algae, sediments	9	3.6	9	9	19.9	0.7
Unidentified organic matter	58	23.3			487.1	17.0
Cannibalism	74	29.7	75	6.2	1943.6	67.7
TOTAL	1205	100	249		2870.66	

in March 2007 and for a total of four stomachs from other samples. Overall, 8.2% were empty, 49% had little trace of food, 22% were half full, 6.4% were almost full, and 14.2% were completely full. Most stomach samples from Santa Rosalia were no more than half full. The relatively large number of full stomachs in October 2006 and November 2007 was due to cannibalism. Stomach fullness index distributions did not significantly differ between three samples taken in July 2006 (Santa Rosalia, San Pedro Martir, and Salsipuedes basins), with most stomachs (≥50%) containing little food (Chi-square test, $\chi^2 = 7.02$, d.f. = 8, $p > 0.05$). The sample of squid

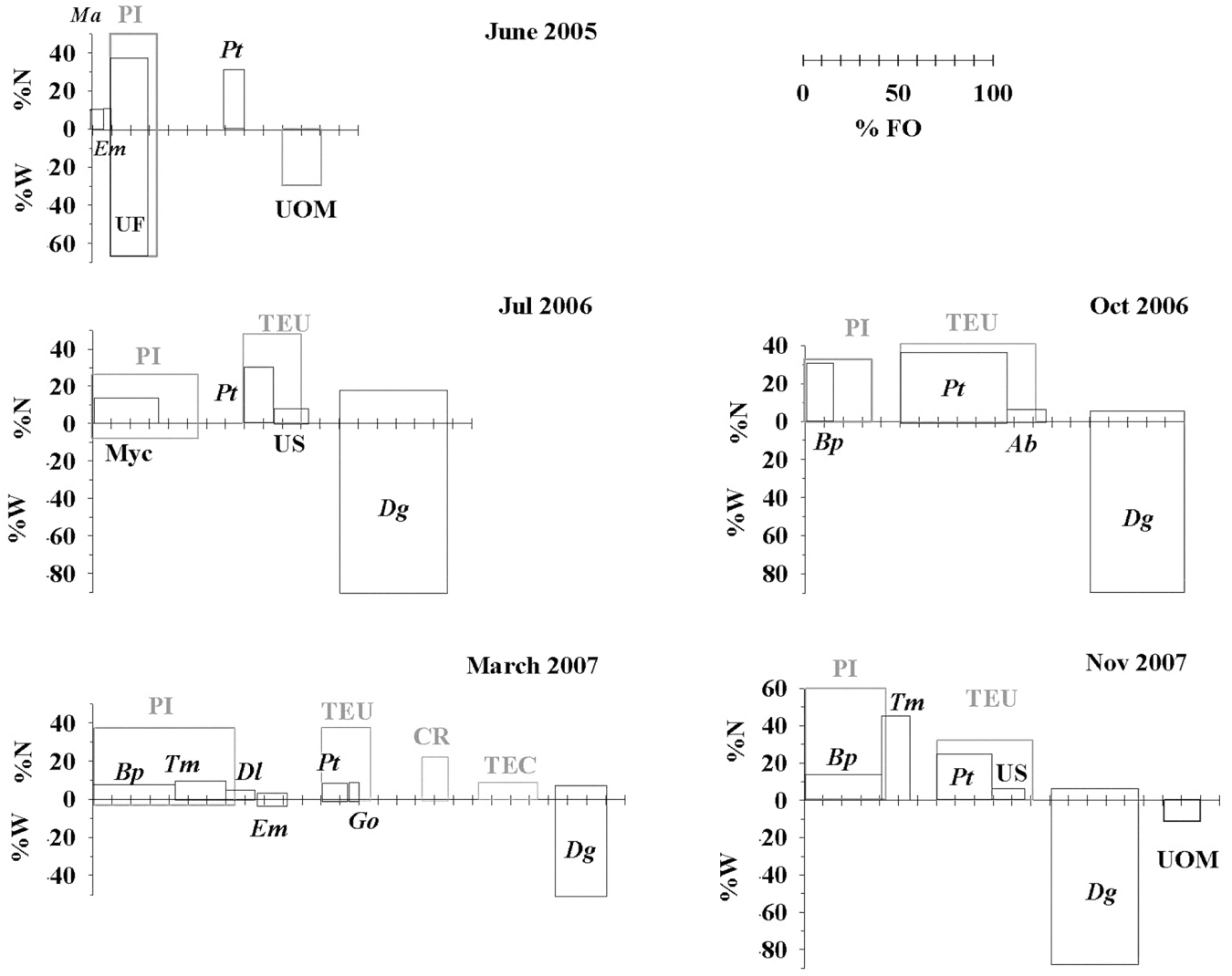

Figure 4. Monthly composition by percentage number (%N) and weight (%W) (vertical axis) and frequency of occurrence (%FO, horizontal axis) of prey found in the stomach contents of jumbo squid (*Dosidicus gigas*) collected off Santa Rosalia, 2005–2007. Myc, Myctophidae; *Bp, Benthosema panamense*; *Tm, Triphoturus mexicanus*; *Dl, Diogenychthys laternatus*; *Ma, Merluccius angustimanus*; *Em, Engraulis mordax*; UF, Unidentified fish; *Pt, Pterygioteuthis giardi*; *Ab, Abraliopsis affinis*; *Go, Gonatus* spp.; US, Unidentified squid; *Dg, Dosidicus gigas*; and UOM, Unidentified organic matter. Large prey groups in grey: PI, Pisces; TEU, Teuthoidea; TEC, Thecosomata; and CR, Crustacea. The illustrated %FO scale applies to all panels (1 small division = 10%).

stranded at Pt. San Marcial was unusual in that half of the stomachs were completely full (fig. 3).

Diet Description

Stomach contents of jumbo squid revealed three main groups of prey: fishes, molluscs (cephalopods and pteropods), and crustaceans (tab. 2). Fishes occurred in over half of the stomachs and accounted for 44 %N. Myctophids were the most abundant and frequent fish and accounted for 31% of all prey, both by number and occurrence. *Benthosema panamense* was the dominant myctophid, accounting for 22 %FO and 17 %N. Another myctophid, *Triphoturus mexicanus*, accounted for 9.2 %FO and 12.7 %N. Similar to the case of myctophids, unidentified teleosts had a 30 %FO and formed a fairly consistent component of the diet in most of the samples (see next section). Although the anchovy, *Engraulis mordax*, has a large %FO in Table 2, it was a significant prey item in only two samples (see below).

Cephalopods were next in importance; they were found in 32% of stomachs, and accounted for 38% of all prey by number. Micronektonic squid, *Pterygioteuthis giardi*, dominated, accounting for 22 %FO and 27 %N. Unidentified cephalopods, represented by lenses with 10 %FO and 8.6 %N, probably belong to *P. giardi* as well. Pteropods and crustaceans were relatively minor com-

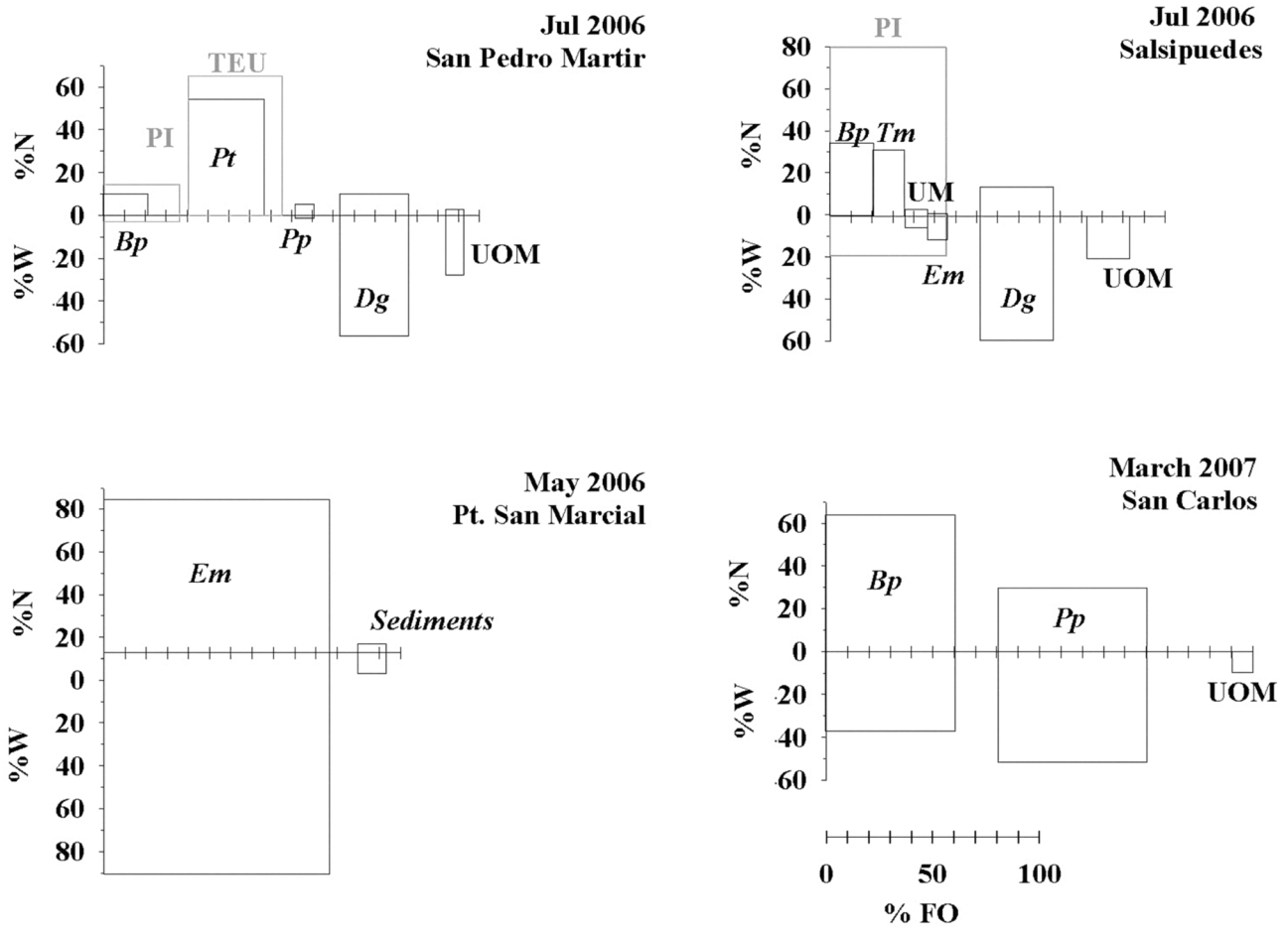

Figure 5. Composition by percentage number (%N) and weight (%W)(vertical axis) and frequency of occurrence (%FO, horizontal axis) of prey found in the stomach contents of jumbo squid (*Dosidicus gigas*) collected in several localities of the central Gulf of California, 2005–07. *Bp, Benthosema panamense*; *Tm, Triphoturus mexicanus*; UM, Unidentified myctophid; *Em, Engraulis mordax*; *Pt, Pterygioteuthis giardi*; *Pp, Pleuroncodes planipes*; *Dg, Dosidicus gigas*; and UOM, Unidentified organic matter. Large prey groups in grey, as in Figure 4.

ponents of stomach contents overall, but the pelagic red crab, *Pleuroncodes planipes*, was a dominant prey species in one sample (see below). Most of the weight of the stomach contents consisted of cannibalized squid (68%) and unidentified organic matter (17%).

Temporal Variation

Temporal variation in jumbo squid diet was assessed over the course of non-consecutive months at Santa Rosalia (fig. 4). The stomach contents of squid taken in June 2005 were dominated by unidentified fish (36 %N and 67 %W), and to a lesser degree by the squid *P. giardi* (31 %FO). In every other sample from this area, an assortment of micronektonic mesopelagic prey dominated the diet. The squid *P. giardi* and other small squids were reasonably abundant, along with myctophids (mostly *B. panamense* and *T. mexicanus*). Myctophids dominated in March 2007 (81 %FO), whereas *P. giardi* was more frequent and abundant in October 2006 (57 %FO and 40 %N). In July 2006 myctophids occurred in 38% of stomachs while *P. giardi* accounted for 33% of all prey by number. In November 2007, *B. panamense* occurred in 39% of stomachs, *T. mexicanus* accounted for 43% of all prey, and *P. giardi* were 39 %FO and 25 %N. While the relative importance of fishes (PI) and squids (TEU) varies, a strong seasonality in diet in the Santa Rosalia area was not evident over this time period (fig. 4), although the abundance of unidentified fish in June 2005 may reflect some seasonal change.

Regional Variation

Diet varied to a much greater degree between different sampling sites than between different time points in Santa Rosalia (fig. 5). A sample from the San Pedro Martir Basin (July 2006) was dominated by micronektonic squid, *P. giardi* (35 %FO and 56 %N), and the myctophid, *B. panamense*. Stomach contents of squid caught in the nearby Salsipuedes Basin at the same time were dominated by fish, myctophids *B. panamense* and *T. mexicanus*, but were totally lacking in the squid, *P. giardi*. In

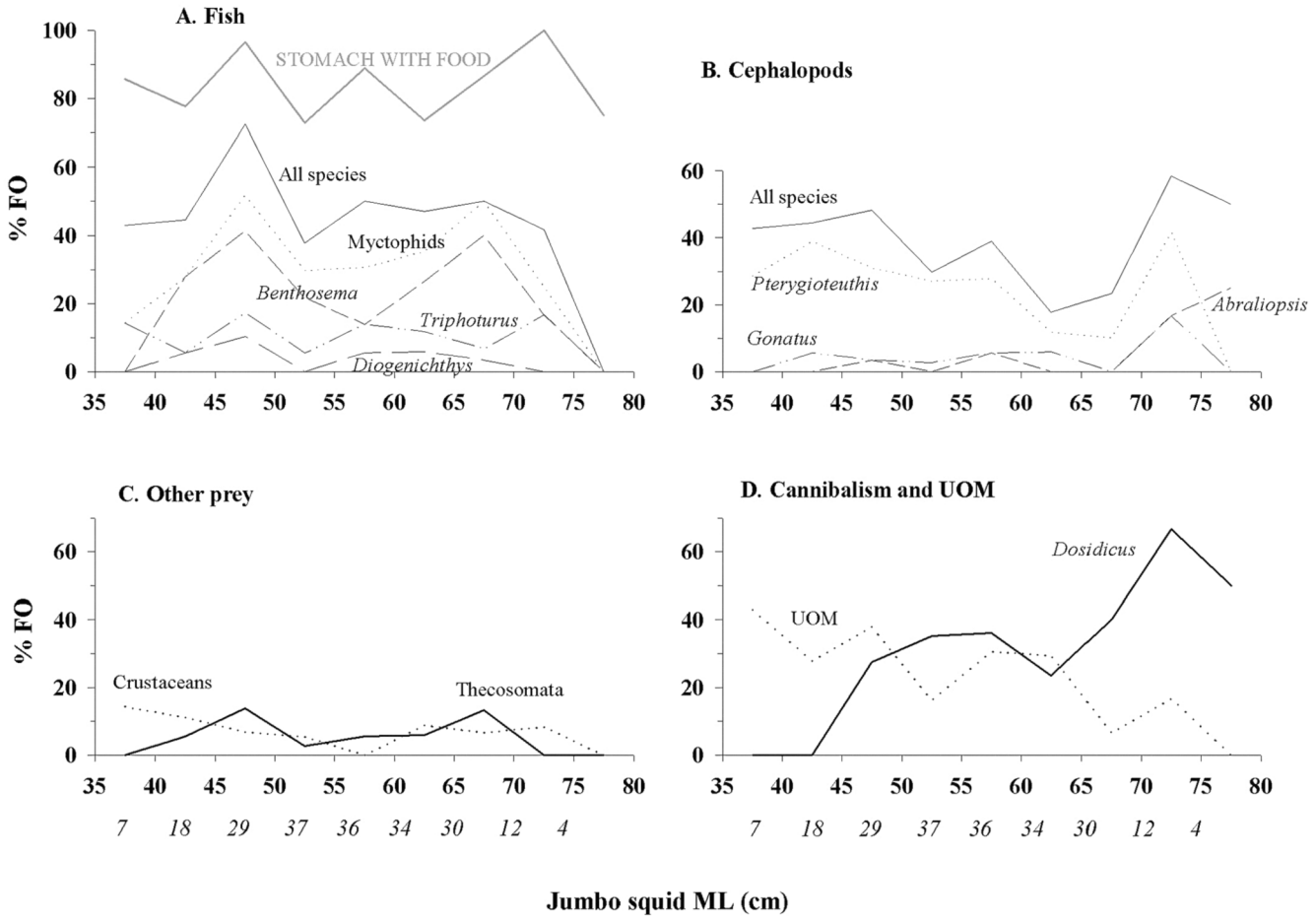

Figure 6. Frequency of occurrence of the most important prey of 207 jumbo squid (*Dosidicus gigas*) from the central Gulf of California during 2005–07 as a function of mantle size: (A) fish, (B) cephalopods, (C) crustaceans and Thecosomata, and (D) cannibalism and unidentified organic matter. Number of squid analyzed per size interval is given in italics at the bottom. Note that the fraction of non-empty stomachs is also plotted in panel A.

both samples, cannibalism accounted for most of the weight. The San Pedro Martir sample is thus quite similar to that collected in Santa Rosalia at the same time, whereas the Salsipuedes sample lacked micronektonic teuthoids.

Squid from San Carlos in March 2007 contained mostly *B. panamense* (60 %FO and 63 %N) and *P. planipes* (70 %FO, 29 %N, and half total weight). Stomachs of squid stranded at Point San Marcial contained only northern anchovy (%FO, %N, and %W ranged from 85–95%) (fig. 5). Both of these samples were qualitatively different from the ones discussed in the paragraph above.

Prey Type Versus Squid Size

Prey occurrence (%FO) versus squid size (35–82 cm ML, at 5 cm ML intervals) for 207 stomachs from the central Gulf of California is shown in Figure 6. Low values of %FO for the largest size interval (>75 cm ML) are skewed by the small number of very large animals. The frequency of empty stomachs varied between 4% and 27% with no clear dependence on ML (complement of "Stomachs with food" in fig. 6). Fishes, mainly myctophids, had moderately high occurrences (37–72%) in jumbo squid of all sizes (fig. 6A). Similarly, consumption of mesopelagic cephalopods, mostly *P. giardi*, is also quite high over the entire size range of squid (17–58%) (fig. 6B). Crustacean and pteropod (Thecosomata) occurrences were relatively low for squid of all sizes (fig. 6C). Although there was no clear dependence of any of these prey items on the size of the squid, cannibalism clearly increased with squid size. One in four squid in the 45–50 cm ML range showed evidence of cannibalism, whereas most squid >70 cm ML were cannibals. Occurrence of unidentified organic matter continuously decreased with squid size, from 42.8 %FO at 35–40 cm ML to 16.6 %FO at 70–75 cm ML (fig. 6D).

Prey Number

Major fish and cephalopod prey types were mainly represented by single occurrences, with numbers ranging from 1 to 10 (fig. 7). But the maximum number for some prey types including *P. giardi* (fig. 7D) was much

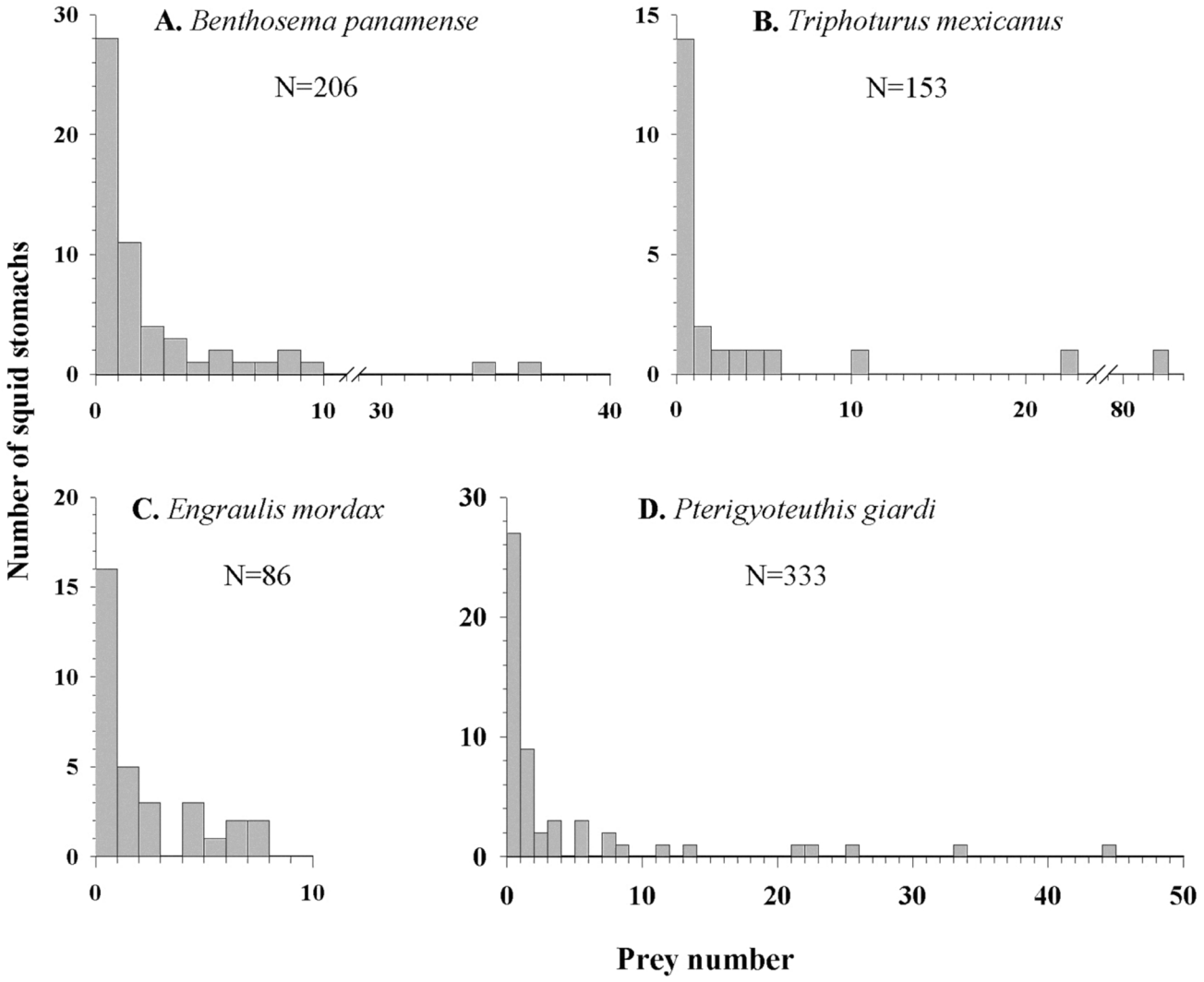

Figure 7. Frequency distributions of the number of prey items found in individual jumbo squid (*Dosidicus gigas*) stomachs from either counts of otoliths pairs for fishes: (A) *Benthosema panamense*; (B) *Thiphoturus mexicanus*; (C) *Engraulis mordax*; or beaks for squid (D) *Pterygioteuthis giardi*. The total number of prey items of each type are indicated on each panel.

larger, ranging from 36 (*B. panamense*, fig. 7A) to 83 (*T. mexicanus*, fig. 7B). Northern anchovy were the exception with a maximum number of eight found (fig. 7C); However, these squid were all quite small, and their stomachs were very full. With the exception of *P. planipes* and thecosomate pteropods (not illustrated), no more than two individuals of any other species were found in any one stomach.

Prey Size Versus Squid Size

Micronektonic myctophids (*B. panamense* and *T. mexicanus*) constituting the main prey of *D. gigas* were 33–66 mm in length, equivalent to 5–20% of jumbo squid ML. Micronektonic squid ranged from 13–37 mm ML, or 2–7% of jumbo squid ML. Weight of myctophids ranged from 0.2–1.5 g, and most squid weighed 0.1–1.8 g. Neritic prey such as northern anchovy ranged from 35–80 mm, equal to 8–30% of squid ML. The largest prey items found in this study were two Panama hakes (*Merluccius angustimanus*) 23 cm in standard length, about half the size of the ML of the squid that consumed them. Weight of these fish were more than 100-fold greater than that of typical micronektonic prey. Cannibalized squid were 16–36 cm ML and 37–64% of the consuming squid's ML (tab. 3). Figures 8A-C illustrate that prey sizes did not show any obvious dependence on the size of the consuming squid.

DISCUSSION

General Features of Diet

Jumbo squid collected by jigging in the central Gulf of California had some generally consistent features in their diet across all sample areas. They tended to forage

TABLE 3
Size of hard remains and estimated dimensions for prey of jumbo squid (*Dosidicus gigas*) from the Gulf of California during 2005–07.

					Estimated prey dimensions						
		Otolith length, mm			Standard length, mm			% Jumbo squid ML			Weight, g
Prey	Number	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.	Range	Range
Fish											
B. panamense	129	2.02	0.21	1.4–2.6	47.4[a]	5.3	32.6–61.7	8.4	1.8	5.6–20.1	0.27–1.5
T. mexicanus	84	0.95	0.13	0.7–1.3	52.5[a]	5.2	42.6–66.3	9.9	1.3	7.2–13.2	0.17–1.1
D. laternatus	6	1.03	0.05	1–1.1							
V. lucetia	6	1.66	0.22	1.4–1.9							
E. mordax	46	2.01	0.53	1.5–3.5	46.8	12.2	35.0–80.6	15.1	5.0	8.2–29.3	7.9–168
M. angustimanus	2	14.9		12.8–17	262		227–229	52.4		52.2–52.6	123–267
Argentina sialis	1	1									
		Lower rostral length, mm			Mantle length, mm						
		Mean	S.D.	Range	Mean	S.D.	Range				
Squid											
P. giardi	172	0.44	0.07	0.2–0.6	20.9	2.6	13–27.7	3.9	0.7	2.1–7.2	0.07–1.6
Gonatus sp.	3	0.70	0.37	0.3–1.1	27.9	7.2	37–19.4	4.6	1.3	3.4–6.3	0.11–1.8
A. affinis	7	1.30	0.08	1.2–1.4	34.8	1.5	33–36.8	5.1	1.0	4.6–7.5	2.80–3.9
Cannibalism	14	5.81	1.76	1.6–7.4	295	66	166–360	54.1	9.1	37–64	9–995

[a]Total length, mm.

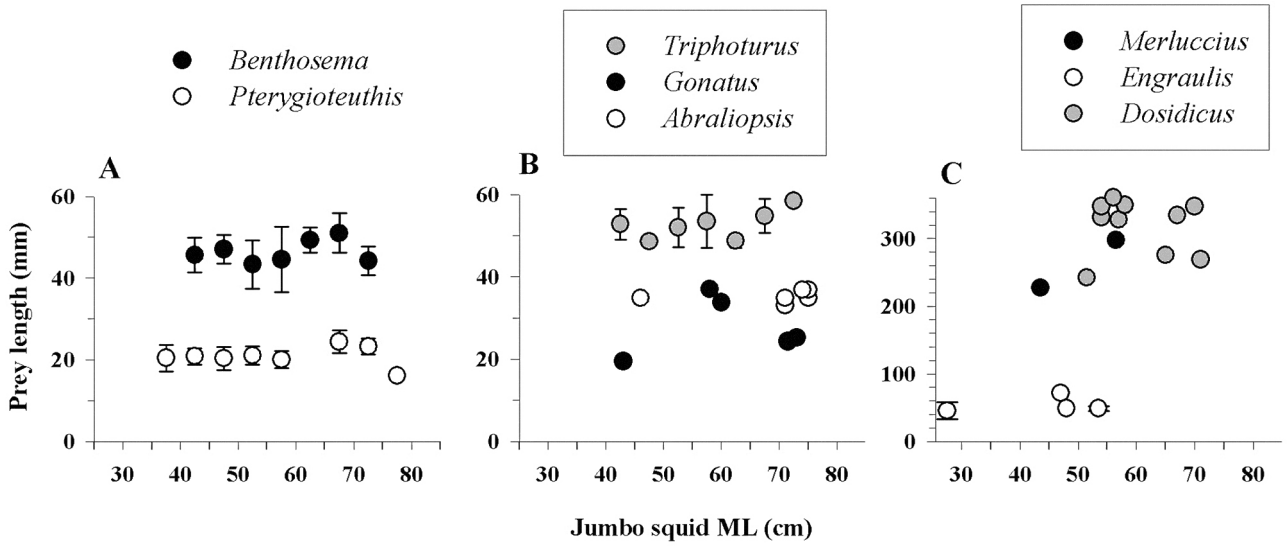

Figure 8. Body length of the most abundant prey found in jumbo squid (*Dosidicus gigas*) as a function of squid ML: (A) *Benthosema panamense* and *Pterygioteuthis giardi*; (B) *Triphoturus mexicanus*, *Gonatus* sp., and *Abraliopsis affinis*; and (C) *Merluccius angustimanus*, *Engraulis mordax,* and *Dosidicus gigas*. Total length is used for myctophids, ML for squid, and standard length for hake and northern anchovy.

primarily on an assortment of mesopelagic micronekton, specifically the myctophid fishes *Benthosema panamense* and *Triphoturus mexicanus*, and the squid *Pterygioteuthis giardi*. These primary prey species were characteristic of all sampling sites within the Guaymas Basin and San Pedro Martir Basin, with the exception of San Carlos, Sonora, where *Pleuroncodes planipes* was also a major prey item. Overall composition of prey species, frequency of occurrence of individual prey species, and size of prey items showed no dependence on squid ML between 40–70 cm, a range that largely makes up the commercial fishery. These results are in general agreement with previous data from the Gulf of California (Markaida and Sosa-Nishizaki 2003; Markaida 2006).

Myctophids are extremely abundant in the central Gulf of California and show a diel vertical migration to near-surface waters at night from daytime depths that are related to the upper boundary of the oxygen minimum layer (OML) (Robison 1972). This hypoxic mesopelagic environment is characteristic of the central

and southern Gulf of California at depths >250 m (Roden 1964; Álvarez-Borrego and Lara-Lara 1991). *T. mexicanus* is commonly associated with acoustic deep-scattering layers (DSL) at 300–400 m depth during daylight in this region (Dunlap 1970; Robison 1972), and this is likely to be the case for other major mesopelagic species comprising the diet of jumbo squid, particularly *B. panamense* and *P. giardi*. DSL communities were well developed during daytime over the upper slope of the Guaymas Basin off Santa Rosalia during our study (unpublished observations), and most of the prey consumed by jumbo squid in this region may thus constitute part of a mesopelagic boundary community (Reid et al. 1991). Recent electronic tagging studies of *Dosidicus gigas* in the Guaymas Basin show that the squid's vertical migrations are consistent with foraging on these species during both day and night (Gilly et al. 2006). Both squid and the DSL community spend daytime at depths associated with the OML and spend much of the night in near-surface waters.

Biases in Stomach Contents Analysis

Several biases may occur when analyzing stomach contents of squid taken by jigging. Cannibalism may be the largest concern, because *Dosidicus gigas* flesh was the most important dietary component by weight. These chunks of squid flesh were always fresh, indicating recent ingestion, and such cannibalistic attacks are commonly observed on impaired squid that are caught by the jig. Such behavior provoked by fishing is clearly unnatural and has been previously discussed (Markaida and Sosa-Nishizaki 2003). It remains unclear to what extent such attacks are launched on other squid in the absence of fishing efforts.

Additionally, hungry squid may be more likely to attack a jig, and this factor could be related to the relatively small number of prey remains often found in individual stomachs. However, squid with full stomachs are also caught by jigs (this paper and Bazzino et al., submitted).

Finally, some species of squid are known to discard the heads from larger fish prey (Collins and Pierce 1996), and identifying these fish by otoliths in the squid stomach would obviously not be possible. There is no evidence that *Dosidicus gigas* discard the heads of the small fishes that have been identified, but some predation on flesh of larger fishes cannot be ruled out.

Diet Variability on the Santa Rosalia Fishing Grounds

Santa Rosalia is the focus of the jumbo squid fishery on the Baja California coast, and this fishery generally runs from April or May until mid- to late-November. Sampling at Santa Rosalia during 2006–07 (March, July, October, and November) in the present study thus covers the entire traditional fishing season, although coverage is incomplete and not from a single season. All samples revealed the assortment of mesopelagic micronekton discussed in the previous section plus a significant amount of other fishes, mostly neritic and pelagic species, although no individual species was ever very abundant. The relative ranking of fish (PI in fig. 4) and squid (TEU) varied between samples, but both were always important by %N and %FO. Thus, there seems to be no marked seasonal variation in the diet of jumbo squid in the Santa Rosalia area, although a more complete sampling throughout the entire fishing season is still lacking.

The only sample from Santa Rosalia that did not fit with this picture was the one from June 2005. This sample was dominated by anchovy and unidentified fishes but still contained some of the standard micronekton seen in every other sample. As discussed below, we propose that this anomaly represents opportunistic feeding and demonstrates the need for systematic sampling to accurately characterize the diet of *Dosidicus gigas*.

Diet in Other Regions of the Central Gulf

More limited sampling in other parts of the Gulf does not allow detailed comparisons to the data from Santa Rosalia, but nonetheless some general points can be made. Two samples from July 2006 collected in the San Pedro Martir Basin and the nearby Salsipuedes Basin also displayed a diet of mixed micronekton similar to that observed in Santa Rosalia. The San Pedro Martir Basin is a northern extension of the Guaymas Basin, and samples from here were most similar. The Salsipuedes sample was also dominated by myctophids and other fishes, but lacked mesopelagic squids.

The latter comparison is particularly interesting. Despite the proximity of the San Pedro Martir and Salsipuedes sampling sites (fig. 1), the midwater physical environments of these areas are quite different because they are separated by a shallow sill (<200 m deep) that prevents mixing. As a result, the San Pedro Martir Basin has a well-developed OML (as do all the basins to the south), whereas the Salsipuedes Basin does not, due to strong tidal mixing and upwelling in the Ballenas Channel (Roden 1964; Álvarez-Borrego and Lara-Lara 1991). Oxygen concentration at the Salsipuedes site was >60 μM at depths of 500 m, compared to concentrations of <20 μM at 400 m depth at the San Pedro Martir sites (W. F. Gilly, unpublished data). Thus, jumbo squid do not appear to require the environment of the OML, at least on a time scale of days (migrations between the sites are possible). *B. panamense* is the most common mesopelagic fish north of the sill but *T. mexicanus* is also present (Robison 1972).

Two other samples are in marked contrast to the above generalization. Another micronektonic prey, *P. planipes*

(pelagic red crab), dominated stomach contents of squid in March 2007 off San Carlos, Sonora. At that time we observed dense schools of *P. planipes* at the surface over depths of 70–215 m between San Pedro Nolasco Island and San Carlos (unpublished observations). Although *P. planipes* is not commonly encountered in most of the central Gulf, large benthic abundances can occur on the upper shelf (at OML depths) along the area between San Pedro Martir Island and San Carlos/Guaymas in spring months (Arvizu-Martinez et al. 1974; Mathews et al. 1974).

P. planipes was previously found in jumbo squid diet during spring 1996 off Guaymas (Markaida and Sosa-Nishizaki 2003), and our observations in March 2007 are consistent with this pattern. Where and when they are available, *P. planipes* is clearly an important supplementary prey species for jumbo squid in the central Gulf. *P. planipes* is much more abundant in the Pacific Ocean, particularly off the southwestern coast of the Baja California peninsula (Boyd 1967), where it is the major prey for many pelagic predators, including jumbo squid (Sato 1974; Markaida 2006; Bazzino et al., submitted).

A second major deviation from the mixed micronekton diet occurred in the sample from Point San Marcial in May 2006. All of these rather small, immature squid had only anchovies in their stomach contents and most stomachs were completely full. Causes for such strandings are unknown (Gilly 2005), but clearly these squid had recently engaged in a mass foraging episode on anchovies. It is unknown how natural this type of feeding behavior is. For whatever reason, these squid had moved inshore to shallow waters from their normal deep habitat. What fraction of this group of squid was actually involved in the stranding is not clear. The comparatively low abundance of anchovy remains in other analyzed stomachs suggests that such feeding is unusual, but it does fit with the idea that *Dosidicus gigas* can be opportunistic.

Diet Stability Versus Opportunism

The diet of jumbo squid in the central Gulf of California, as exemplified by that observed in Santa Rosalia, is clearly dominated by mesopelagic micronekton, primarily myctophids and small squids that constitute mesopelagic boundary communities on the slopes of the Guaymas Basin as well as more northern basins such as San Pedro Martir. This mesopelagic assemblage typically resides in the upper boundary of the OML during the daytime and migrates to near-surface waters at night. It provides a reliable source of assorted micronekton, and hypoxia-tolerant jumbo squid probably continuously forage on these organisms over their entire vertical range (Gilly et al. 2006).

During the course of a traditional fishing season in Santa Rosalia (April/May to November) this pattern appears to be relatively stable, and diet does not vary appreciably during this period. Most squid are thought to leave the Santa Rosalia area by December and move to the winter fishing grounds off Guaymas (Markaida et al. 2005) or to other regions of the Gulf, possibly including San Pedro Martir (Gilly et al. 2006). At present, the connection between this seasonal exodus of jumbo squid from the Santa Rosalia area and the availability of the relevant local micronekton is unknown, but changes in the mesopelagic communities (Markaida 2006) or environmental factors (Markaida and Sosa-Nishizaki 2001) could be involved. Seasonal shifts in upwelling-driven primary productivity occur in this region as well, with productivity falling in winter along the Baja coast and rising along the Sonora coast (Roden 1964; Álvarez-Borrego and Lara-Lara 1991).

In contrast with this general pattern of stable foraging, *D. gigas* also shows a highly opportunistic mode of feeding that demonstrates great plasticity. In the present study this is most dramatically demonstrated by the selective feeding on anchovies that might cause them to strand at Point San Marcial (May 2006). Similarly, jumbo squid in the San Carlos/Guaymas area significantly supplement their diet of mesopelagic fare with *P. planipes*, an abundant but ephemeral springtime prey species. To a lesser extent, opportunistic foraging undoubtedly is responsible for consumption of the larger neritic and pelagic fish species listed in Table 2, neither of which substantially contribute to %N or %FO.

We propose that *D. gigas* routinely takes advantage of foraging opportunities in both ways discussed above. In Santa Rosalia a locally stable resource of mesopelagic micronekton represents a primary attraction to jumbo squid, but they still take advantage of unpredictable opportunities to forage on other neritic and small pelagic fishes. Archival tagging data indicate that jumbo squid tend to leave the tagging site on the shelf off Santa Rosalia after a few days and move over deeper offshore waters (Gilly et al. 2006). We suggest that these horizontal movements are associated with explorations for improved foraging grounds and that during such forays opportunistic foraging may be particularly common. A pattern like this has also been observed on the shelf outside Magdalena Bay on the Pacific coast, where jumbo squid consumed pelagic red crabs and an assortment of fishes as well as myctophids (Bazzino et al., submitted).

Relevance to *Dosidicus gigas* Diet in Other Locations

Samples in recent years have consistently shown that the mesopelagic micronekton (mainly myctophids) of the Guaymas Basin in the Gulf of California can sustain a population of *Dosidicus gigas* on a year-round basis since the fishery resumed in 1994 (Markaida and Sosa-

Nishizaki 2003; Markaida 2006; this study). It is thus likely that patterns observed in this core region of the central Gulf are relevant elsewhere. In particular, the balance between stable and opportunistic foraging is likely to be critical in determining how long jumbo squid will remain in a given area. The most extensive data set relevant to this question comes from the Pacific Ocean off California in conjunction with the recent northward range expansion of this species (Field et al. 2007). Jumbo squid off central California consume large numbers of myctophids and other small mesopelagic organisms, but they also forage heavily on a variety of fairly large fishes, including hake, rockfish (*Sebastes* spp.), anchovy, and sardine. Maximum size of prey items is also substantially larger in the more northern waters.

Although these fishes may be attractive prey, it is unlikely that foraging on such relatively slow-growing and long-lived species (relative to *D. gigas*) alone could be maintained on the long-term in a given locality. Indeed, a reciprocal relationship between hake abundance and jumbo squid abundance in Monterey Bay, California, has been suggested based on unmanned submersible operations over the last decade (Zeidberg and Robison 2007). Even in such highly productive areas, a diet of mesopelagic micronekton, particularly myctophids, is likely to be far more sustainable. Given the highly migratory nature of jumbo squid, opportunistic explorations from a relatively stable center would appear to be an effective strategy, both in the Guaymas Basin and elsewhere.

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OVERVIEW OF THE CHILEAN HAKE (*MERLUCCIUS GAYI*) STOCK, A BIOMASS FORECAST, AND THE JUMBO SQUID (*DOSIDICUS GIGAS*) PREDATOR-PREY RELATIONSHIP OFF CENTRAL CHILE (33°S–39°S)

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ABSTRACT

Total Chilean hake (*Merluccius gayi*) landings from off central Chile (33°–39°S) declined from 120,000 t in 2004 to 40,000 t in 2007. This paper evaluates the impacts of both fishing and *Dosidicus gigas* predation relative to the observed collapse of *M. gayi*. We provide a brief review of the state of *M. gayi* stock using population indicators. In addition, we evaluate the predator-prey interaction between *D. gigas* and fishing to explain changes observed in the *M. gayi* stock in recent years using a dynamic food web model. Estimates of predation mortality suggest that cannibalism in *M. gayi* is more important than predation by *D. gigas*. In addition, a decline in length at catch, in the proportion of mature females, and in the catch per unit of effort in the *M. gayi* fishery has been observed since summer 2000, i.e., three years before the outbreak of *D. gigas* in central Chile. We projected the *M. gayi* biomass using two Ecopath models describing the system in 2000 and 2005 and the software Ecopath with Ecosim. The increase in *D. gigas* biomass resulted in a slow decrease in *M. gayi* biomass from 2000 to 2010. Fishing scenarios resulted in a decrease in *M. gayi* biomass from 2004 (juveniles) and from 2003 (adults).

INTRODUCTION

Historically, Chilean hake (*Merluccius gayi*) has been the main fishing resource for human consumption in Chile, with production exported mainly as frozen filets. The *M. gayi* fishery is considered fully-exploited[1]; from 1975 to 1986 annual landings were below 40,000 tons, and slowly increased to a maximum of approximately 150,000 t in 2001. Landings declined in 2002 and 2003, decreasing rapidly back to 40,000 tons in 2007 (fig. 1).

Although the National Fishery Council (NFC) in Chile set the total allowable catch (TAC) for the *M. gayi* fishery at 62,000 t for 2007, the advice from Subsecretaría de Pesca (Undersecretary of Fishery, SubPesca) was to catch only 50,000 t (SubPesca 2006). However, statistics from the Servicio Nacional de Pesca (National Fishery Service; www.sernapesca.cl) indicate that only the industrial sector (vessels greater than 1,000 hp) achieved its quota (ca. 37,000 t), while the artisan sector (long-liners with fishing gear not larger than 10,000 hooks) landed only 3,000 t out of a 25,000 t allocation. This was attributed primarily to the reduced availability of *M. gayi* (Lillo et al. 2005) in the coastal waters where the artisan boats operate.

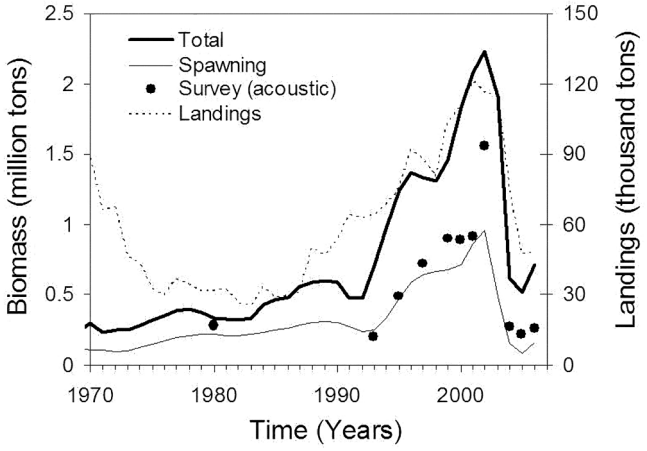

Figure 1. Landings and stock biomass of *Merluccius gayi* off central Chile from 1970 to 2006.

This decline in landings since 2004 has resulted in a loss of about 1,500 direct jobs in fishing companies. As a comparison, each direct job in the industrial sector (e.g., members of crews, workers in frozen fishing companies) supports four indirect jobs (services like transport, food supply, restoration of nets and electronic equipments, among others). In addition, in the artisanal sector approximately 5,000 fishermen left the fishery between 2005 and 2007 (Dresdner pers. comm.[2]) The consequences of these declines have been increasing conflict among stakeholders (e.g., managers and representatives of workers in fishing companies, and artisan fishers) and the Fishing Authority. In interviews and opinion articles in the local press, stakeholders used economic and social reasons to protest against any potential decrease in the annual TAC.

[1]Based on the Chilean Fishing and Aquaculture Law N° 18,892 and subsequent amendments (www.subpesca.cl).

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The *M. gayi* stock was managed using a statistical stock assessment model (SubPesca 2006) that indicated that the *M. gayi* biomass peaked in 2002 with ca. 2.2 million t (Payá 2006; fig. 1). This assessment was based on an age-structured model calibrated with biomass estimates from acoustic surveys. The *M. gayi* biomass estimated during the acoustic survey in 2002 reached 1.6 million t, 70% greater than the biomass estimated in 2001 (917,000 t). There was no acoustic survey conducted in 2003, and the subsequent survey in 2004 estimated only 272,000 t, a decrease by one order of magnitude with respect to 2002. We considered the unusual nature of the 2002 point estimate in Arancibia and Neira (2003) and Arancibia[3] has presented an unpublished analysis on the subject. However, Payá (2006) and SubPesca (2006) related the drastic drop in the *M. gayi* biomass in 2004 (see fig. 1) to "a catastrophic event of unknown origin, likely predation by jumbo squid (*Dosidicus gigas*)." More recently, Arancibia et al. (2007) reviewed available life-history data for *D. gigas* (age, growth, maturity, reproduction, and mortality, among others) and estimated *D. gigas* consumption of *M. gayi*.

Several factors may be responsible for the significant drop of *M. gayi* biomass off central Chile. The aim of this paper is to evaluate the impacts of both fishing and *D. gigas* predation relative to the observed collapse of *M. gayi*. We provide a brief review of the state of *M. gayi* stock using population indicators. In addition, we evaluate the predator-prey interaction between *D. gigas* and fishing to changes observed in the stock of *M. gayi* in recent years, using a dynamic food web model.

MATERIALS AND METHODS

The overview of the *M. gayi* stock was conducted with a meta-analysis using a time series of biological indicators that cover the period 1997–2007. The indicators were monthly mean length, inmature/mature ratio, and catch per unit of effort (Alarcón unpubl. data[4]). The aim is to analyze population signals in the *M. gayi* stock before and after 2002–03, which is the period of the *D. gigas* invasion.

The study area corresponds to the upwelling system off central Chile (fig. 2) located in the southern section of the Humboldt Current System, one of the four major eastern boundary ecosystems of the world. The study area supports high levels of primary productivity (19.9 g C/m^2/d; Daneri et al. 2000) and globally significant landings (>4.5 million t in 1995). The models represent the marine area that extends from 33°S to 39°S and from the coastline to 30 nm westward, covering a total area of approximately 50,000 km^2. This is a relatively independent ecological and geographical unit (Camus 2001) characterized by a narrow continental shelf (<30 nautical miles), strongly seasonal upwelling (September to March), and high levels of primary productivity (Strub et al. 1998; Daneri et al. 2000; Escribano et al. 2003).

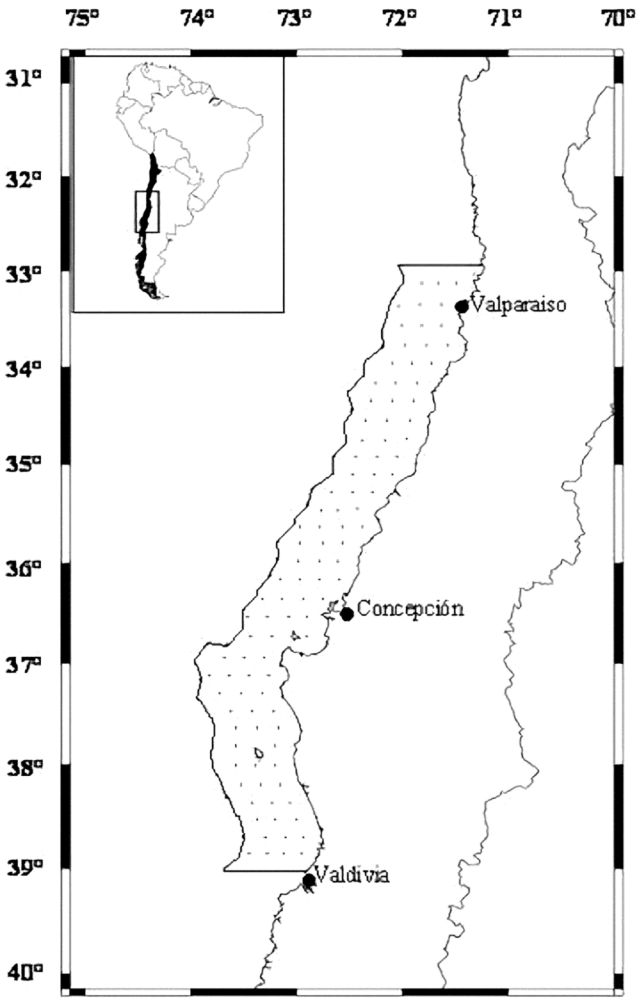

Figure 2. Study area.

In terms of the main biological components, the study area sustains a diverse and productive food web (Neira and Arancibia 2004; 2007; Neira et al. 2004). The phytoplankton group is dominated by large diatoms for most of the year, while the zooplankton group is dominated by herbivorous copepods and euphausiids. Jellyfish also constitute an important group in the plankton domain. Macrocrustaceans are significant benthic components and some species such as red squat lobster (*Pleuroncodes monodon*), yellow squat lobster (*Cervimunida johni*), and pink shrimp (*Heterocarpus reedi*) support important fisheries. The finfish community is dominated by pelagic

[3]Arancibia, H. Analysis of the interaction between jumbo squid and common hake using an ecotrophic post-modern method: EwE. Talk to the National Fishing Council of Chile (original in Spanish). Valparaíso, September 4th, 2007 (www.subpesca.cl).

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species; small pelagic fishes such as anchovy (*Engraulis ringens*) and the endemic common sardine (*Strangomera bentincki*), in particular, are present at high biomass levels off central Chile and dominate landings. Horse mackerel (*Trachurus symmetricus*) is another important resource in the study area. This highly migratory species performs large-scale migrations in the Pacific Ocean. The demersal fish community is dominated by Chilean hake (*M. gayi*) both in biomass and landings.

To evaluate the relative influence of fishing and *D. gigas* predation on *M. gayi* dynamics from 2000 to 2010, we used a food-web approach. We used two Ecopath (Christensen and Pauly 1992) models (with 31 functional groups) that represent the upwelling system off central Chile in 2000 (before the *D. gigas* invasion; Neira and Arancibia 2007; Appendices 1 and 2) and 2005 (after the invasion of *D. gigas*; Arancibia and Neira unpubl. data; Appendices 3 and 4). The models include age structure in groups where enough data are available to split adult and juvenile stages. Based on Arancibia (1987), *M. gayi* juveniles are those in age groups 0–3 years old, while adults are 4+ years old. For *S. bentincki*, *E. ringens*, and *P. monodon*, we considered juveniles to be age 0 fish (recruits) and adults to be age 1+.

The data sources used to parameterize the models are described in Arancibia et al. (2007) and Neira and Arancibia (2007). Using the model representing the system in 2000, we performed the following series of simulations using the Ecopath with Ecosim software, EwE (Walters et al. 1997):

(i) *D. gigas* biomass from 2000 to 2005 was increased by one order of magnitude. This was conducted in EwE assuming a biomass accumulation rate (Ba) of 1.66/year for *D. gigas*.

(ii) The observed fishing mortality ($F = Y/B$) of *M. gayi* from 2000 to 2005 was applied based on the stock assessment results.

(iii) Based on Arancibia and Neira (2003), a fishing mortality coefficient was applied to *M. gayi* which was corrected for discards and underreported catch. This corresponds to a 30% increase in *F*.

(iv) Scenario (i) was independently combined with scenarios (ii) and (iii).

Later, we performed two extra sets of simulations using the model representing the system in 2005 where:

(v) Fishing mortality of *M. gayi* was constant (i.e., $F = F_{2005}$) from 2005 to 2010;

(vi) $F = 0$ from 2005 to 2010;

(vii) $F = F_{2005}$ from 2005 to 2007, and $F = 0$ from 2008 to 2010.

We introduced the EwE main equations and hypotheses (for more details on model equations and assumptions see Christensen and Pauly 1992; Walters et al. 1997; and Christensen et al. 2005). EwE is a software that allows mass balance snapshots (Ecopath) and time dynamics (Ecosim) to be constructed using direct and indirect trophic relationships in any food web. Ecopath is based on two equations. The first balances the new production of each group, *i*, into removals by fisheries, predators, unexplained mortality, migration, and biomass trends:

$$P_i = Y_i + B_i \cdot M2_i + BA_i + E_i + P_i \cdot (1–EE_i), \quad (1)$$

where P_i is total production, Y_i is total fishery catch, B_i is biomass, BA_i is biomass accumulation, $M2_i$ is total predation rate, E_i is net migration rate (emigration - immigration), and P_i $(1–EE_i)$ is other mortality ($M0_i$), based on the ecotrophic efficiency (*EE*) which represents the total fraction of the production that is either eaten by predators or exported from the system, including in the form of fishery catch.

Following Winberg (1956), the second main equation in EwE expresses the mass balance for each group *i* of the system as:

$$Q_i = P_i + R_i + U_i, \quad (2)$$

where Q_i is prey consumption both inside and outside the system (imports), P_i must be eaten by predators, exported from the system, or contributed to detritus, R_i is respiration, and U_i is unassimilated food.

In Ecopath, the term describing predation mortality ($M2$) is calculated as follows:

$$M2_i = \sum_{j=1}^{n} Q_j \cdot DC_{ji}, \quad (3)$$

where the summation is over all *n* predators feeding on the prey *i*, Q_j is the consumption ratio of predator *j*, DC_{ji} is the diet composition of predator *j* (i.e. proportion in weight of prey *i* in the stomach content of predator *j*) which is calculated as follows:

$$Q_j = B_j \cdot (Q/B)_j, \quad (4)$$

Ecosim is the time-dynamic version of the Ecopath model and uses mass-balance results from Ecopath for parameter estimation. Differential and difference equations are used in Ecosim to simulate the dynamics of fast- and slow-growing groups. The model explicitly incorporates the effects of trophic controls and allows for limited size/age structure (Walters et al. 1997). In Ecosim, the biomass changes for functional groups are functions of biomass, harvest rate, other mortalities, and predator consumption (for more detailed equations see Walters et al. 1997; Pauly et al. 2000; Christensen and Walters 2004; Christensen et al. 2005):

$$\frac{dB_i}{dt} = f(B_i) - M0_i B_i - F_i B_i - \sum_{j=1}^{n} c_{ij} \cdot (B_i, B_j), \quad (5)$$

where $f(B)$ is a positive function of biomass *B* for each

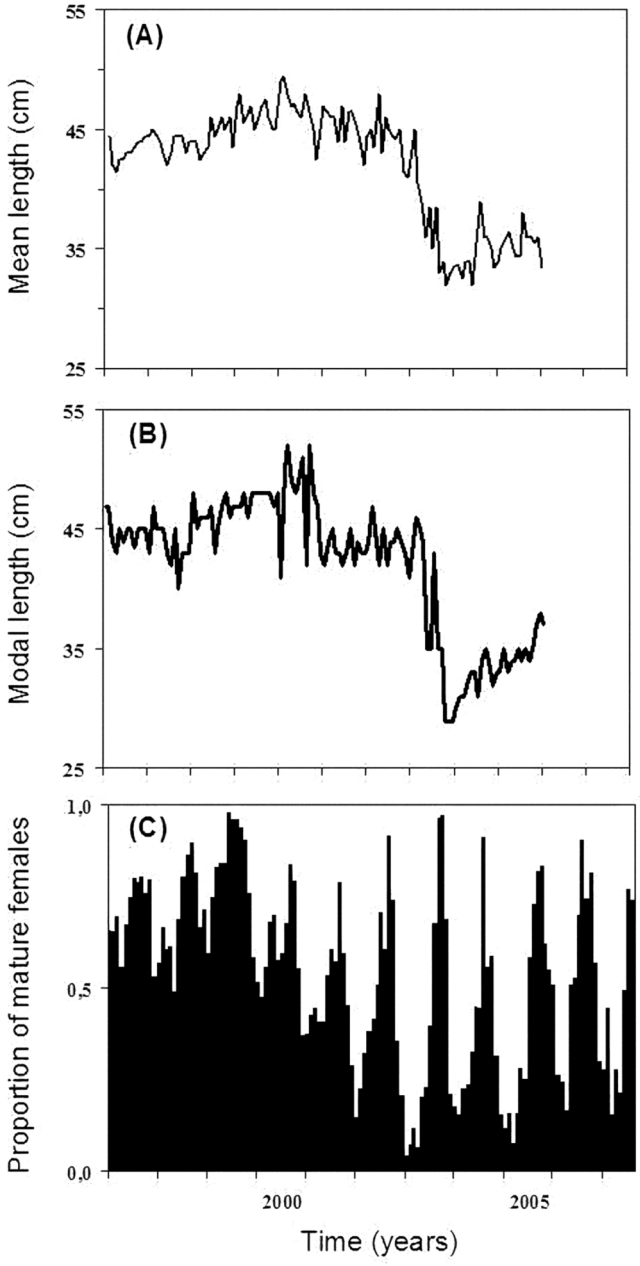

Figure 3. Stock indicators of *Merluccius gayi* (males and females combined) for the years 1997–2007. (A) mean of total length; (B) model of total length; (C) proportion of mature females.

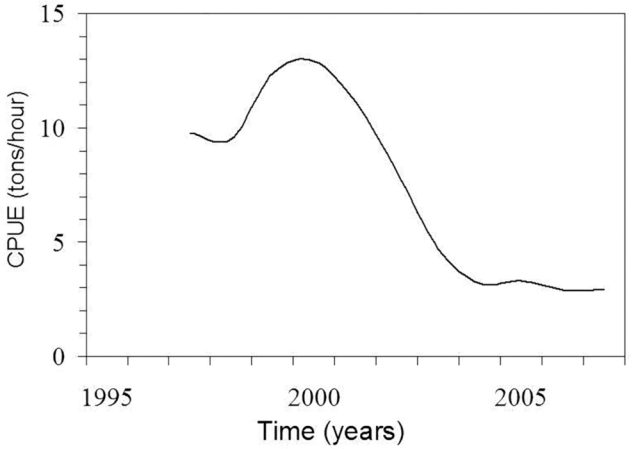

Figure 4. Non-standardized catch per unit of effort (CPUE) of the industrial trawling fleet targeting *Merluccius gayi* off central Chile.

group i in the model, $M0_i$ is a non-predator mortality rate, F_i is the fishing mortality rate, and $c_{ij}(B_i,B_j)$ is a function that predicts consumption of prey i by predator j.

Predator-prey interactions in Ecosim are assumed to be moderated by prey behavior to limit exposure to predation (vulnerability), and overall food web dynamics can show either bottom-up or top-down control (Walters et al. 1997; Christensen et al. 2005). In the absence of further knowledge, we used default values for the vulnerability parameters as well as the maximum P/B ratio, feeding and handling time for all predator-prey interactions.

RESULTS

The monthly average length of *M. gayi* (combined sexes) is shown in Figure 3A. The indicator increased from early 1997 to late 2000, then slightly declined until 2003, and dropped until mid 2005. The modal length in catch follows the same trend as the monthly average length, but the contrast is more apparent (fig. 3B). The proportion of mature females in *M. gayi* shows strong seasonality, with mature females being more abundant in the second half of any year (fig. 3C). However, the proportion of immature individuals increased from 1999 to 2005 (the slight decrease in the percentage of immature females in 2004 may be linked to greater availability of larger females during sampling). The proportion of immature females in catches was high until 2007, but recruitment has been relatively low in more recent years (SubPesca 2006).

The non-standardized CPUE of the industrial trawling fleet targeting *M. gayi* was at a maximum in 2000, quickly dropping from 2001 to 2004 and staying very low until 2007 (fig. 4). Raw CPUEs previous to 1998 have not been estimated.

Results from the mass-balanced models are shown in Figures 5A and B (mortality coefficients) and Figure 5C (removed biomass). In terms of juvenile mortality coefficients, the biggest changes between the two models were observed in predation mortality (strongly decreased) and "other mortalities" (those that increased). In *M. gayi* adults, fishing mortality (F) and predation mortality ($M2$) increased, while "other mortalities" ($M0$) decreased from 2000 to 2005.

Figure 5C shows comparisons of *M. gayi* biomass (juveniles and adults combined) removed by *M. gayi* (can-

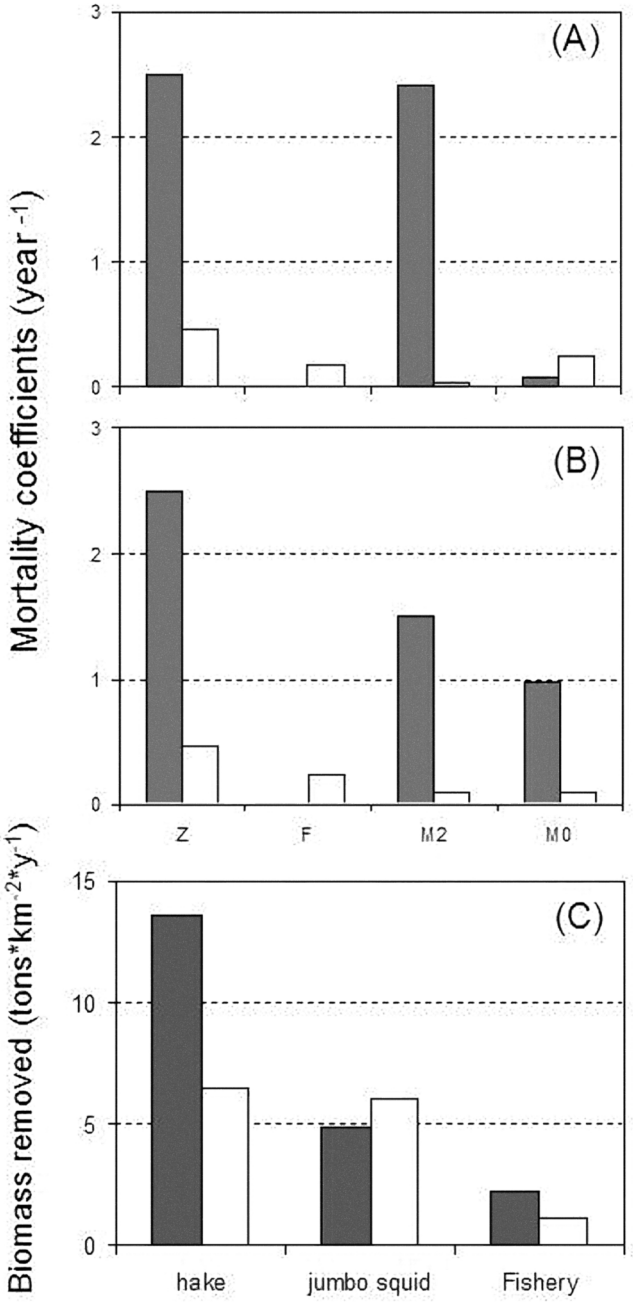

Figure 5. Ecopath-based indicators from two models off central Chile. Mortality coefficients in *M. gayi* calculated for (A) year 2000 and (B) year 2005; grey bars: juveniles (0 to 3 years old); white bars: adults (4+). (C) comparison of *Merluccius gayi* biomass (adults and juveniles) removed by *M. gayi*, *Dosidicus gigas* and the fishery in 2000 (grey bars) and 2005 (white bars).

nibalism), *D. gigas* (predation), and the fishery (catch). In the two analyzed periods, *M. gayi* removed the most *M. gayi* biomass, followed by *D. gigas*, and then the fishery. However, in 2005 *M. gayi* and the fishery removed about 50% of what they removed in 2000, and *D. gigas* removed about 10% more compared to 2000.

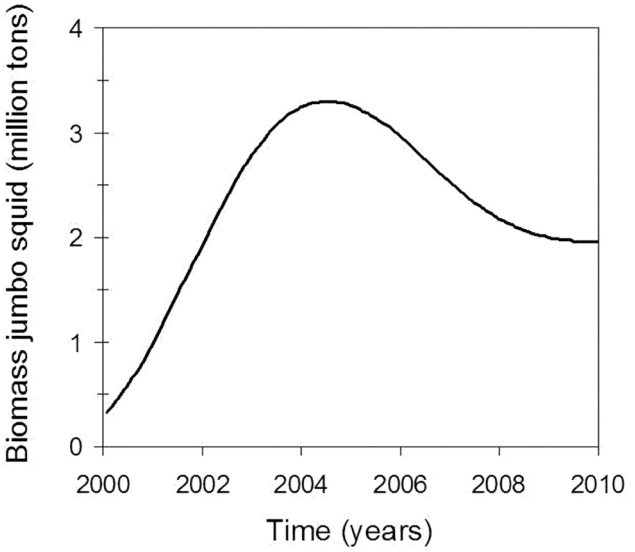

Figure 6. Simulated trend in the biomass of *Dosidicus gigas* from 2000 to 2010.

Results from simulated scenarios using EwE are shown in Figures 6 and 7. In Figure 6 we show the biomass of *D. gigas* simulated by assuming a biomass accumulation rate of 1.66/year using the model representing the system in 2000. The biomass of *D. gigas* increased from 2000 to 2005 (maximum) and then decreased until 2010.

Figures 7A and 7B show the *M. gayi* biomass trend (juveniles and adults) under several fishing and predation scenarios. The simulated increase in *D. gigas* biomass led to a slow decrease in *M. gayi* biomass (adults and juveniles) from 2000 to 2010. Fishing scenarios led to a decrease in *M. gayi* biomass starting in 2004 for juveniles and in 2003 for adults. The strongest effects were found when fishing and *D. gigas* predation were combined, with *M. gayi* biomass decreasing by 30% in juveniles and 40% in adults in 2000.

Trends in the biomass of *M. gayi* under several scenarios of fishing mortality (2005–10) are shown in Figures 7C and D. Applying a constant fishing mortality $F = F_{2005}$ from 2005 to 2010 did not result in observable changes in the *M. gayi* biomass (juveniles and adults). $F = 0$ from 2005 to 2010 would have resulted in a recovery of 20% in juveniles and more than 50% in adults. The simulation of $F = F_{2005}$ from 2005 to 2007 and $F = 0$ from 2007 to 2010 led to a recovery in the biomass of *M. gayi* juveniles (10%) and adults (35%).

DISCUSSION

The results of our evaluation of the key biological and fishery indicators for the *M. gayi* stock off central Chile (33°–39°S) (fig. 3) suggest that fishing was the primary (driving) factor behind the observed decline in the stock. The decline in CPUE was matched by a decline

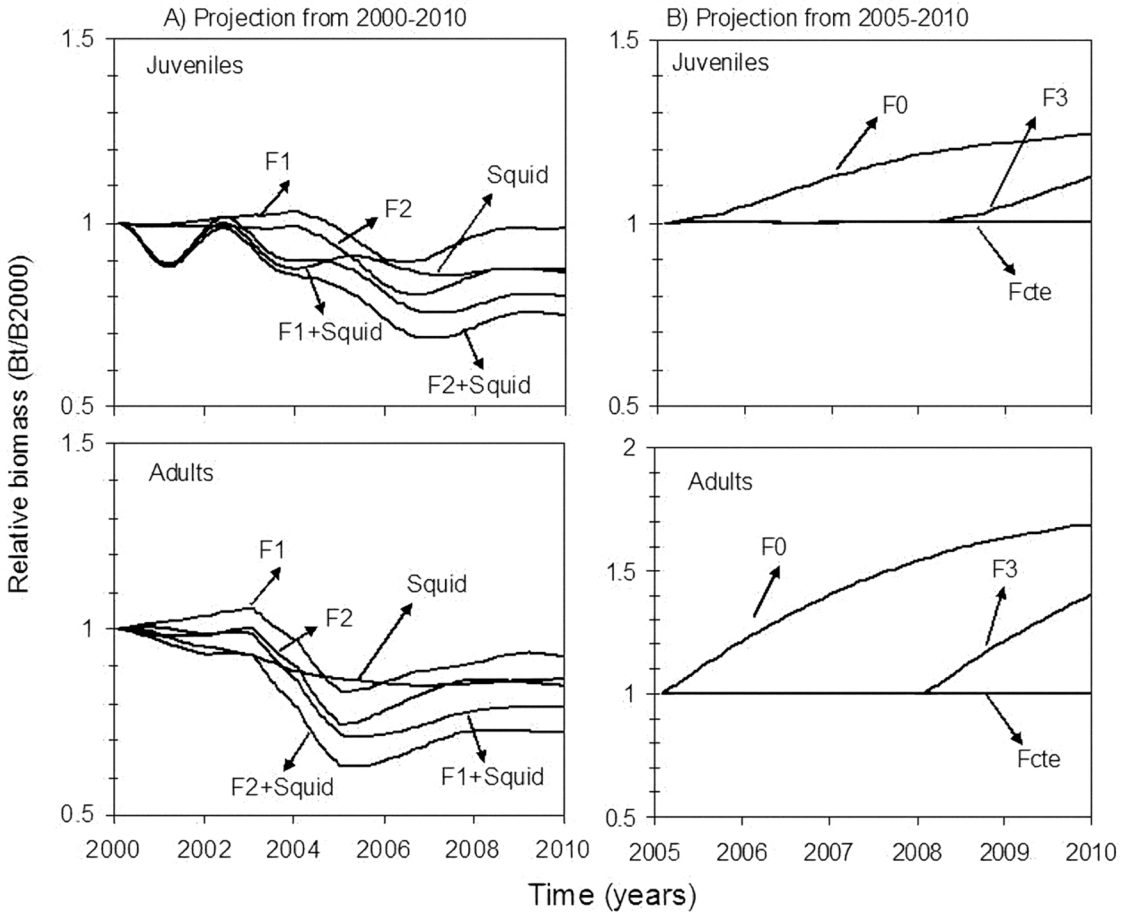

Figure 7. Trends in the *Merluccius gayi* biomass under several scenarios simulated using Ecopath models built in this study. (A) Projection from 2000 to 2010; (B) Projection 2005–10. F = fishing mortality; F1 = official fishing mortality (F = Y/B) 2000-2005; Squid: increase in the *Dosidicus gigas* biomass; F2 = corrected fishing mortality (see text); F1+Squid: combination of official fishing mortality and increase in *D. gigas* biomass; F2+Squid = combination of fishing mortality (corrected) and increase in *D. gigas* biomass; Fcte = F_{2005} constant; F0 = no fishing from 2005 to 2010; F3 = F_{2005} applied from 2005 to 2007 and then no fishing from 2008 to 2010.

in the mean total length of *M. gayi* catch as well as a rapid decline in the percentage of mature females. This indicates a decrease in the reproductive potential of the stock since 2000, two years before the maximum relative abundance (CPUE) of *D. gigas* was observed. This suggests that management control rules failed to protect the stock from overexploitation. The continuous increase in annual landings of *M. gayi* from the mid 1980s to mid 2000s (fig. 1) resulted in stock depletion below target biomass levels. Consequently, we recommend that the basic biological data for the *M. gayi* stock and its fishery be reviewed and evaluated based on the indicators that we have discussed here.

The comparison between ecotrophic models (for 2000 and 2005, see Appendices 1 and 2) indicated that an important decrease in predation mortality in *M. gayi* juveniles occurred between 2000 and 2005 (figs. 5A, B). This change is explained by the decrease in cannibalism, which in turn is explained by the decrease in the adult stock biomass. This is in agreement with Arancibia et al. (1998), who reported that *M. gayi* adults are opportunistic predators that cannibalize juveniles (mainly prerecruits, i.e., individuals of age-group 0 with total length less than 12 cm). Later, Jurado-Molina et al. (2006) also reported similar results, that *M. gayi* juveniles represent more than 90% of cannibalized individuals.

Model results indicate that in 2000, *D. gigas* removed about one third of what was removed by cannibalism in *M. gayi*. In 2005, removal by *D. gigas* was still lower than that by cannibalism, even when the adult stock of *M. gayi* was decimated (fig. 5C). It does not seem likely that catastrophic *D. gigas* predation on *M. gayi* (sensu Payá 2006; and SubPesca 2006) occurred since predation by *D. gigas* was lower than cannibalism in *M. gayi* in both models for 2000 (previous to the collapse of the fishery operating on *M. gayi*) and 2005 (after the collapse).

During the time periods considered here, the most *M. gayi* biomass was removed by cannibalism, followed by *D. gigas* predation, and then the fishery. However, in 2005, *M. gayi* and the fishery removed about 50% of the

biomass that they removed in 2000, while removal by *D. gigas* increased by about 10% compared to 2000 (fig. 5C). Therefore, the most parsimonious explanation for the observed changes in *M. gayi* biomass are changes in cannibalism and fishing, rather than *D. gigas*.

The EwE approach assumes that the vulnerability of individuals to predation within a life-history period is independent of size or age. Under this assumption, cannibalism in *M. gayi* is a bigger source of mortality than *D. gigas* predation. However, there is a hypothetical situation when *D. gigas* could exert strong top-down trophodynamic control on smaller (younger) individuals within a life-history period. Under these conditions, and with the same total consumption rate of juvenile *M. gayi* by *D. gigas*, the age-specific mortality rates of *M. gayi* would be extraordinarily high in the size/age ranges affected both by cannibalism and *D. gigas* predation, and for which cohort biomass was relatively small. There is no evidence of such strong trophic control of *D. gigas* on *M. gayi* off central Chile, and therefore our simulations did not explore the effect of changes in vulnerability of *M. gayi* life-history periods. However, the effects of predation and cannibalism on different *M. gayi* life-history periods could be explored in future studies.

Our simulations indicated that, all else being equal, an increase in *D. gigas* biomass by one order of magnitude would lead to a slow decrease in *M. gayi* biomass (adults and juveniles) from 2000 to 2010. By contrast, fishing scenarios based on assessment estimates of fishing mortality led to a noticeable decrease in *M. gayi* biomass from 2004 (in juveniles) and 2003 (in adults), which is consistent with the observed dynamics of the *M. gayi* stock before 2004 (fig. 1). The greatest declines in hake biomass were observed when the effects of fishing and *D. gigas* predation were combined, with declines of 30% (juveniles) and 40% (adults) relative to the *M. gayi* biomass in 2000. However, the simulated increase in *D. gigas* may be overestimated, as it is based on a biomass increase of one order of magnitude from 2000 to 2005, which, due to the highly uncertain data, may be unlikely (fig. 8).

The simulations may have captured fishing effects (fig. 7) because they included estimates of discards in the industrial trawling and underreported catch reported (Arancibia and Neira 2003). Arancibia and Neira (2003) estimated that underreported catch in the industrial *M. gayi* fishery was 20% of the official landing (www.sernapesca.cl). This value has historically been estimated at 12%, but was raised to 20% after 2000 due to Law N° 19,713, when maximum individual transferable quotas by owner of fishing vessels were implemented.

The last set of simulations (fig. 7) indicate that if the *M. gayi* fishery were to be managed using levels of fishing mortality (F) similar to those observed in 2005, the stock would be expected to remain at low biomass levels. These simulations indicate that had the fishery been closed in 2005 ($F = 0$), then recovery of the stock would be expected to take place from 2005 to 2010. In Chile, some stakeholders agree with the idea of a temporary moratorium for the *M. gayi* fishery, however more widespread support for this closure has so far been impracticable due to social impacts (such as job loss). Arancibia and Cubillos (1993) previously evaluated options for protecting the spawning biomass of *M. gayi*, and recommended a threshold of 225,000 t as a management limit. By contrast, the spawning biomass of *M. gayi* in 2006 was as low as 140,000 t (SubPesca 2006).

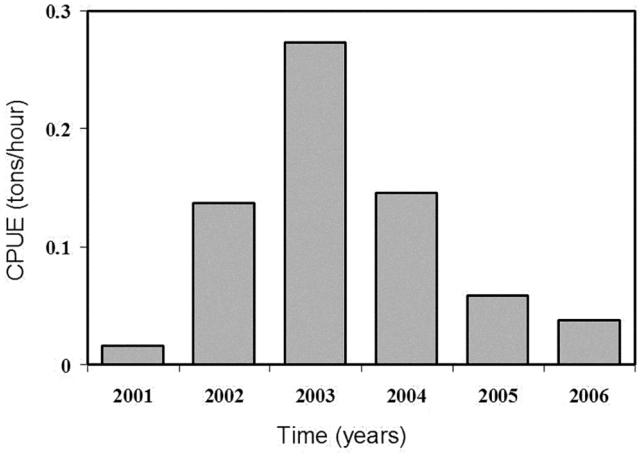

Figure 8. Catch per unit of effort (ton/hour) of *Dosidicus gigas* as by-catch in the trawling fishery of *Merluccius gayi* off central Chile, from 2001–06 (data source: Arancibia et al. 2007).

A question that remains is how the biomass of a demersal species of low growth (von Bertalanfy growth coefficient K = 0.1 – 0.2/y; www. fishbase.org) could increase by 70% in one year (e.g., from 2001 to 2002) in the absence of good recruitment and in the presence of exploitation. The doubling time for this species is about three years and therefore an increase in biomass in 2002 seems unlikely. Consequently, it is possible that the acoustic survey in 2002 was affected by anomalous behavior of *M. gayi* or misidentification of acoustic signals with other co-occurring fish species. There is some indirect evidence to suggest that *M. gayi* could have been erroneously identified during the acoustic survey, as the species dominating the study area during 2002 was hoki (*Macruronus magellanicus*). In fact, the density of hoki increased 15 times from 2001 (1.25 t/km^2) to 2002 (19.04 t/km^2), decreasing again in 2004 (1.98 t/km^2) as measured in an acoustic survey (Lillo, S. pers. commun.[5]).

Our analysis suggests that the *M. gayi* stock has been affected by overfishing since 2000, as indicated by a decline in catch per unit of effort, length of catch, and the

[5]Lillo, S. Pers. commun. Instituto de Fomento Pesquero, P.O. Box 8-V, Valparaíso, Chile. Email: slillo@ifop.cl.

proportion of mature females in the stock. These are typical effects of fishing and cannot be ascribed to predation since *D. gigas* prey primarily on juvenile *M. gayi* (Arancibia et al. 2007). In addition, any strong predation by *D. gigas* would have been expected to occur primarily since 2003 (when the maximum *D. gigas* abundance was observed), and observed in the adult biomass only three to four years later. We suggest that it is unlikely that *M. gayi* biomass almost doubled in one year, as indicated by the acoustic data and assessment model, and it is consequently very likely that the abundance was never as high as was estimated. If this is true, then catastrophic predation by *D. gigas* is not needed to explain the drop in *M. gayi* biomass. We propose that, although potentially important, predation by *D. gigas* is unlikely to have been the driving factor in *M. gayi* population dynamics since 2000. Therefore, we suggest that the idea of catastrophic predation of *D. gigas* on *M. gayi* lacks biological and ecological support.

Results and conclusions from this study may be affected by unavoidable uncertainties associated with the available data and assumptions in ecosystem models. For example, although abundant data are available for determining diets and consumption rates of *M. gayi* adults and for cannibalism, both in the short and long term (Arancibia 1987; Arancibia et al. 1998; Cubillos et al. 2003), data on diet and other important trophodynamic parameters of predators such as jumbo squid are less available (e.g., Arancibia et al. 2007). Moreover, the starting values for estimating jumbo squid abundance are poorly known, and for this exercise are based on top-down model estimates. Therefore, more ecosystem-based research is strongly needed in order to understand and model strong predator-prey interactions and fishing effects on fishing resources in this very productive food web.

ACKNOWLEDGEMENTS

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APPENDIX 1

Inputs (bold) and outputs of the balanced model representing the upwelling system off central Chile in 2000.

Group/Parameter	B	P/B	Q/B	EE	P/Q	F	M2	M0
cetaceans	**0.01**	**0.60**	**10.00**	0.17	0.06	0.00	0.10	0.50
sea lions	**0.07**	**0.25**	**20.00**	0.38	0.01	0.00	0.10	0.16
marine birds	**0.07**	**0.50**	**20.00**	0.00	0.03	0.00	0.00	0.50
hake (j)	**8.57**	**2.50**	**8.32**	0.97	0.30	0.01	2.42	0.08
hake (a)	**12.19**	**0.46**	**5.16**	0.46	0.09	0.18	0.03	0.25
sardine (j)	**41.36**	**1.45**	14.53	0.36	**0.10**	0.21	0.32	0.93
sardine (a)	**14.60**	**1.88**	18.75	0.37	**0.10**	0.32	0.38	1.18
anchovy (j)	**23.97**	**0.70**	7.03	0.77	**0.10**	0.15	0.39	0.16
anchovy (a)	**14.63**	**2.12**	21.20	0.32	**0.10**	0.31	0.37	1.44
squid	3.34	**3.50**	10.61	**1.00**	**0.33**	0.00	3.50	0.00
jumbo squid	**6.50**	**1.75**	**5.00**	1.14	0.35	0.00	1.00	0.75
mesopelagic fish	56.05	**1.20**	**12.00**	**1.00**	0.10	0.00	1.20	0.00
red s. lobster (j)	0.22	**5.90**	**18.00**	**1.00**	0.33	0.00	5.89	0.01
red s. lobster (a)	0.48	**3.57**	**12.50**	**1.00**	0.29	0.17	3.40	0.00
yellow s. lobster	**0.08**	**3.57**	**11.60**	0.85	0.31	0.77	2.27	0.53
pink shrimp	**0.40**	**2.50**	**12.00**	0.47	0.21	0.22	0.94	1.33
horse mackerel	**23.98**	**0.56**	**14.20**	0.36	0.04	0.13	0.07	0.36
hoki	**21.90**	**0.53**	5.28	0.30	**0.10**	0.07	0.09	0.37
sword fish	0.64	**0.50**	5.00	**0.75**	**0.10**	0.38	0.00	0.13
congers	**0.30**	**0.70**	3.50	0.35	**0.20**	0.23	0.02	0.45
rattail fish	0.65	**0.70**	3.50	**1.00**	**0.20**	0.00	0.70	0.00
flat fishes	0.47	**0.70**	3.50	**1.00**	**0.20**	0.00	0.70	0.00
cardinal fish	**0.78**	**0.70**	3.50	0.29	**0.20**	0.15	0.06	0.50
sand perch	**0.05**	**0.70**	3.50	0.10	**0.20**	0.07	0.00	0.63
skates	**0.25**	**0.36**	2.41	0.13	**0.15**	0.05	0.00	0.32
polychaetes	**1.89**	**2.41**	**15.90**	0.00	0.15	0.00	0.00	2.41
jellies	7.77	**0.58**	**1.42**	**0.15**	0.41	0.00	0.09	0.50
copepods	84.71	**45.00**	**154.52**	**1.00**	0.29	0.00	44.96	0.05
euphausiids	68.79	**13.00**	31.71	**1.00**	**0.41**	0.00	12.99	0.01
phytoplankton	364.23	**120.00**	—	**0.30**	—	0.00	36.00	84.00

APPENDIX 2

Diet composition of the predators in the balanced model representing the upwelling system off central Chile in 2000.

Prey/Predator	cetaceans	sea lions	marine birds	hake (j)	hake (a)	sardine (j)	sardine (a)	anchovy (j)	anchovy (a)	squid	jumbo squid	mesopelagic fish	red s. lobster (j)	red s. lobster (a)	yellow s. lobster	pink shrimp	horse mackerel	hoki	sword fish	congers	rattail fish	flat fishes	cardinal fish	sand perch	skates	polychaetes	jellies	copepods	euphausiids
cetaceans	0.010																												
sea lions	0.098																												
marine birds																													
hake (j)	0.060	0.250	0.100	0.040	0.170					0.050	0.150									0.013				0.065					
hake (a)	0.070	0.200	0.050																	0.036									
sardine (j)	0.098	0.180	0.284	0.118						0.050	0.073																		
sardine (a)	0.034	0.065	0.100	0.042							0.072																		
anchovy (j)	0.056	0.110	0.165	0.070						0.050	0.066																		
anchovy (a)	0.036	0.062	0.101	0.042							0.069																		
squid	0.150		0.040		0.002					0.210								0.035	0.010										
jumbo squid	0.150		0.040		0.002						0.070							0.035	0.010										
mesopelagic fish	0.098		0.120		0.300					0.100	0.470						0.025	0.180											
red s. lobster (j)				0.015	0.002															0.004	0.030	0.020			0.002				
red s. lobster (a)				0.008	0.001															0.107	0.110	0.300			0.210				
yellow s. lobster					0.002															0.002		0.020			0.023				
pink shrimp					0.006																								
horse mackerel	0.100	0.100																	0.480										
hoki											0.010								0.500										
sword fish																													
congers		0.004																											
rattail fish					0.002						0.010																		
flat fishes											0.010																		
cardinal fish		0.030																											
sand perch																													
skates																													
polychaetes																													
jellies																	0.002												
copepods						0.020	0.020	0.020	0.020	0.440		0.400					0.002										0.500	0.200	0.400
euphausiids				0.500	0.506					0.100		0.600					0.971	0.750					0.500	0.679					
phytoplankton						0.980	0.980	0.980	0.980																		0.500	0.800	0.600
detritus													1.000	1.000	1.000	1.000										1.000			
Import	0.040			0.165	0.008															0.838	0.860	0.660	0.500	0.256	0.765				
Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

APPENDIX 3

Inputs (bold) and outputs of the balanced model representing the upwelling system off central Chile in 2005.

Group/Parameter B	P/B	Q/B	EE	P/Q	F	M2	M0	
cetaceans	**0.01**	**0.60**	**10.0**	0.167	0.06	0.00	0.10	0.50
sea lions	**0.07**	**0.25**	**20.0**	0.381	0.01	0.00	0.10	0.16
marine birds	**0.07**	**0.50**	**20.0**	0.000	0.03	0.00	0.00	0.50
hake (j)	**9.40**	**2.50**	**8.3**	0.609	0.30	0.02	1.51	0.98
hake (a)	**3.80**	**0.46**	**5.2**	0.777	0.09	0.25	0.10	0.10
sardine (j)	**16.67**	**1.45**	14.5	0.726	**0.10**	0.22	0.84	0.40
sardine (a)	**16.37**	**1.88**	18.8	0.322	**0.10**	0.21	0.39	1.27
anchovy (j)	**18.80**	**0.70**	7.0	**0.999**	**0.10**	0.19	0.52	0.00
anchovy (a)	**16.03**	**2.12**	21.2	0.293	**0.10**	0.23	0.39	1.50
squid	2.27	**3.50**	10.6	**0.999**	**0.33**	0.00	3.50	0.00
jumbo squid	**7.99**	**1.75**	**5.0**	0.718	0.35	0.55	0.71	0.49
mesopelagic fish	35.13	**1.20**	**12.0**	**0.999**	0.10	0.00	1.20	0.00
red s. lobster (j)	0.22	**5.90**	**18.0**	**0.999**	0.33	0.00	5.89	0.01
red s. lobster (a)	0.40	**3.57**	**12.5**	**0.999**	0.29	0.00	3.57	0.00
yellow s. lobster	**0.52**	**3.57**	**11.6**	0.041	0.31	0.00	0.15	3.42
pink shrimp	**0.39**	**2.50**	**12.0**	0.172	0.21	0.13	0.30	2.07
horse mackerel	1.57	**0.56**	**14.2**	**0.999**	0.04	0.45	0.11	0.00
hoki	**15.07**	**0.53**	5.3	0.118	0.10	0.03	0.03	0.47
sword fish	**0.01**	**0.50**	5.0	0.000	**0.10**	0.00	0.00	0.50
congers	**0.30**	**0.70**	3.5	0.027	**0.20**	0.00	0.02	0.68
rattail fish	0.63	**0.70**	3.5	**0.999**	**0.20**	0.00	0.70	0.00
flat fishes	0.29	**0.70**	3.5	**0.999**	**0.20**	0.00	0.70	0.00
cardinal fish	0.06	**0.70**	3.5	**0.999**	**0.20**	0.00	0.70	0.00
sand perch	**0.05**	**0.70**	3.5	0.000	**0.20**	0.00	0.00	0.70
skates	**0.25**	**0.36**	2.4	0.000	**0.15**	0.00	0.00	0.36
polychaetes	**1.89**	**2.41**	**15.9**	0.000	0.15	0.00	0.00	2.41
jellies	0.51	**0.58**	**1.4**	**0.150**	0.41	0.00	0.09	0.50
copepods	41.06	**45.00**	**154.5**	**0.999**	0.29	0.00	44.96	0.05
euphausiids	29.72	**13.00**	31.7	**0.999**	**0.41**	0.00	12.99	0.01
phytoplankton	184.49	**120.00**	—	**0.300**	—	0.00	36.00	84.00

APPENDIX 4

Diet composition of the predators in the balanced model representing the upwelling system off central Chile in 2005.

Prey/Predator	cetaceans	sea lions	marine birds	hake (j)	hake (a)	sardine (j)	sardine (a)	anchovy (j)	anchovy (a)	squid	jumbo squid	mesopelagic fish	red s. lobster (j)	red s. lobster (a)	yellow s. lobster	pink shrimp	horse mackerel	hoki	sword fish	congers	rattail fish	flat fishes	cardinal fish	sand perch	skates	polychaetes	jellies	copepods	euphausiids
cetaceans	0.010																												
sea lions	0.098																												
marine birds																													
hake (j)	0.060	0.250	0.100	0.040	0.170					0.050	0.150									0.013				0.065					
hake (a)	0.070	0.200	0.050																	0.036									
sardine (j)	0.098	0.180	0.284	0.118						0.050	0.073																		
sardine (a)	0.034	0.065	0.100	0.042							0.072																		
anchovy (j)	0.056	0.110	0.165	0.070						0.050	0.066																		
anchovy (a)	0.036	0.062	0.101	0.042							0.069																		
squid	0.150		0.040		0.002					0.210								0.035	0.010										
jumbo squid	0.150		0.040		0.002						0.070							0.035	0.010										
mesopelagic fish	0.098		0.120		0.300					0.100	0.470						0.025	0.180											
red s lobster (j)				0.015	0.002															0.004	0.030	0.020			0.002				
red s. lobster (a)				0.008	0.001															0.107	0.110	0.300			0.210				
yellow s. lobster					0.002															0.002		0.020			0.023				
pink shrimp					0.006																								
horse mackerel	0.100	0.100																	0.480										
hoki											0.010								0.500										
sword fish																													
congers		0.004																											
rattail fish					0.002						0.010																		
flat fishes											0.005																		
cardinal fish		0.030																											
sand perch																													
skates																													
polychaetes																													
jellies																	0.002												
copepods						0.020	0.020	0.020	0.020	0.440		0.400					0.002										0.500	0.200	0.400
euphausiids				0.500	0.506					0.100		0.600					0.971	0.750					0.500	0.679					
phytoplankton						0.980	0.980	0.980	0.980																		0.500	0.800	0.600
detritus													1.000	1.000	1.000	1.000										1.000			
Import	0.040			0.165	0.008						0.005									0.838	0.860	0.660	0.500	0.256	0.765				
Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Part III

SCIENTIFIC CONTRIBUTIONS

A HYPOTHESIS ON RANGE EXPANSION AND SPATIO-TEMPORAL SHIFTS IN SIZE-AT-MATURITY OF JUMBO SQUID (*DOSIDICUS GIGAS*) IN THE EASTERN PACIFIC OCEAN

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ABSTRACT

Dosidicus gigas is a fast growing predator in the eastern Pacific Rim with a high energy demand. Since 2000, it has been found in waters beyond its until-then-known northern and southern distribution limits. At the same time, specimens in the southern hemisphere were observed to reach maturity at significantly larger sizes. Spatio-temporal differences in temperature and food abundance may explain population changes in maturation, growth, and migration. Size-at-maturity depends on temperature and food availability, meaning jumbo squid will mature at smaller sizes under warm conditions and at larger sizes that can migrate longer distances in cool conditions. In this paper, we present the hypothesis that the present invasion of jumbo squid into formerly uninhabited areas was the result of a combination of favorable environmental conditions and fishery impacts: the regime shift from warm to cool water following a strong La Niña/El Niño combined with the fisheries' impact on competitors and predators of *D. gigas* opened up a previously unavailable niche, or "loophole," and allowed for the present spatial expansion of jumbo squid.

INTRODUCTION

The jumbo squid, *Dosidicus gigas*, is a migratory and voracious predator of the eastern Pacific Ocean with high abundances in the southern area of the California Current system and in the northern region of the Humboldt Current system (Roper et al. 1984). It has a high energy demand that is satisfied by unspecific feeding upon prey items that are 5% to 25% the size of its dorsal mantle length (ML), although bigger prey have been reported. In cannibalistic feeding, a commonly observed behavior for jumbo squid, prey size may reach up to 87% of the predators' ML (Markaida and Sosa-Nishizaki 2003). Jumbo squid hunt in small groups (Nigmatullin et al. 2001) and, although they are extreme generalists, it has been shown that myctophids and euphausiids often comprise an important percentage in the diet of juveniles and adults (Markaida 2006a; Blasković et al. 2007). Large females can have as many as 32 million eggs (normally 0.3–13 million eggs are found), which is the highest fecundity among cephalopods (Nigmatullin et al. 2001). Although not universally accepted (Masuda et al. 1998), *D. gigas*, like most other cephalopods, is thought to exhibit "cephalopod senescence" (Anderson et al. 2002) and is semelparous, that is, it does not regress developed reproductive organs but dies after the first spawning or the first spawning sequence (Nigmatullin et al 2001). Like other cephalopods, it does not develop a true larval phase but hatches after three to 10 days as a paralarva (Yatsu et al. 1999), a life stage very similar to the subsequent adult stage. Jumbo squid have a monthly growth rate of up to 8 cm in mantle length (ML) during the paralarvae and the following juvenile stages, and grow up to 6 cm per month in later stages. This is the highest growth rate reported for all cephalopod species (Nigmatullin et al. 2001; Markaida et al. 2005) and enables jumbo squid to reach the reported maximum mantle lengths of up to 120 cm in a lifespan of just a few to 18 months (Nigmatullin et al. 2001).

Until the end of the last millennium, the jumbo squid's northern and southern distribution limits were found at around 30°N and 40°S, with the highest abundances located in the Gulf of California and in waters off Peru (Nigmatullin et al. 2001). A recent RAPD-genetic analysis of eight locations in Mexico, Peru, and Chile indicated that the jumbo squid sub-populations from the two hemispheres are genetically separated, probably because the equatorial currents and counter-currents form a natural barrier (Sandoval-Castellanos et al. 2007).

Various traits of its life history, like shifts in size-at-maturity, cannibalism, and range expansion, give *D. gigas* an extremely plastic response to the highly variable oceanic habitats within the eastern boundary upwelling systems.

Jumbo squid size-at-maturity is highly variable and several authors (e.g., Nesis 1983; Nigmatullin et al. 2001) have proposed three different size-at-maturity strategies in its distribution in the eastern Pacific Ocean (EPO): a

group found in the center of its EPO distribution that matures at a small size; a group throughout the whole distribution area that matures at a medium size; and a group in the northern and southern distribution limits that matures at large size. In Peruvian waters, these groups have not yet been identified from the available oceanic industrial and coastal artisanal fisheries data. Only a small-maturing group and a large-maturing group, which generally correspond to the medium- and the large-sized groups classified by Nigmatullin et al. (2001), can be distinguished (fig. 1) and appear to be both spatially and temporally separated (Argüelles et al. 2008). The terms "small" and "large" in the present study refer to the two size-at-maturity groups found in the Peruvian waters; when we refer to Nigmatullin et al.'s (2001) group classification, this is explicitly mentioned. In the Peruvian exclusive economic zone (EEZ), from 1989 through 1999 (except 1992–93) only specimens of the small size-at-maturity group were caught, whereas, after a transition period in 1999–2000, only specimens thought to belong to the large group were caught (fig. 1).

Statolith analyses revealed that the longevity of mature individuals collected by observers in the industrial fishery in the Peruvian EEZ ranged from around 120 to 350 days according to their size (Masuda et al. 1998; Argüelles et al. 2001). A temporal change in size-at-maturity has also been found for the jumbo squid population in the Gulf of California, where, in a three-year period after the 1997–98 El Niño, the size-at-maturity varied considerably from large to small or medium (Markaida 2006b; Bazzino et al. 2007). Although these groups may belong to genetically different sub-populations (Nesis 1983), no work has been published on the origin or an underlying cause for the existence of these groups.

Cannibalistic feeding is a common behavior among cephalopod species (Amaratunga 1987) and this has been confirmed in stomach content analyses of *D. gigas* from the Gulf of California (Markaida 2006a) and Peruvian waters (Blasković et al. 2007). Among other things, cannibalism reduces intraspecific competition for food and mating under conditions of reduced food availability or very high population densities, allows larger specimens to maintain their food intake over time, and therefore, to increase their fitness (Polis 1981). The cannibalistic weight percentage of all stomach contents of specimens caught by the industrial fishery on jumbo squid in Peruvian waters from 2004 to 2006 (n = 1930; 30–112 cm ML) reached 75% (IMARPE unpubl. data). Although this high rate of cannibalism may be partly due to stress during fishing (Markaida and Sosa-Nishizaki 2003; Ibáñez et al. 2008) and although it may reflect a systematic bias because only larger individuals were captured, it suggests a "population energy storage" strategy: energy is built up during favorable ecosystem conditions by increasing

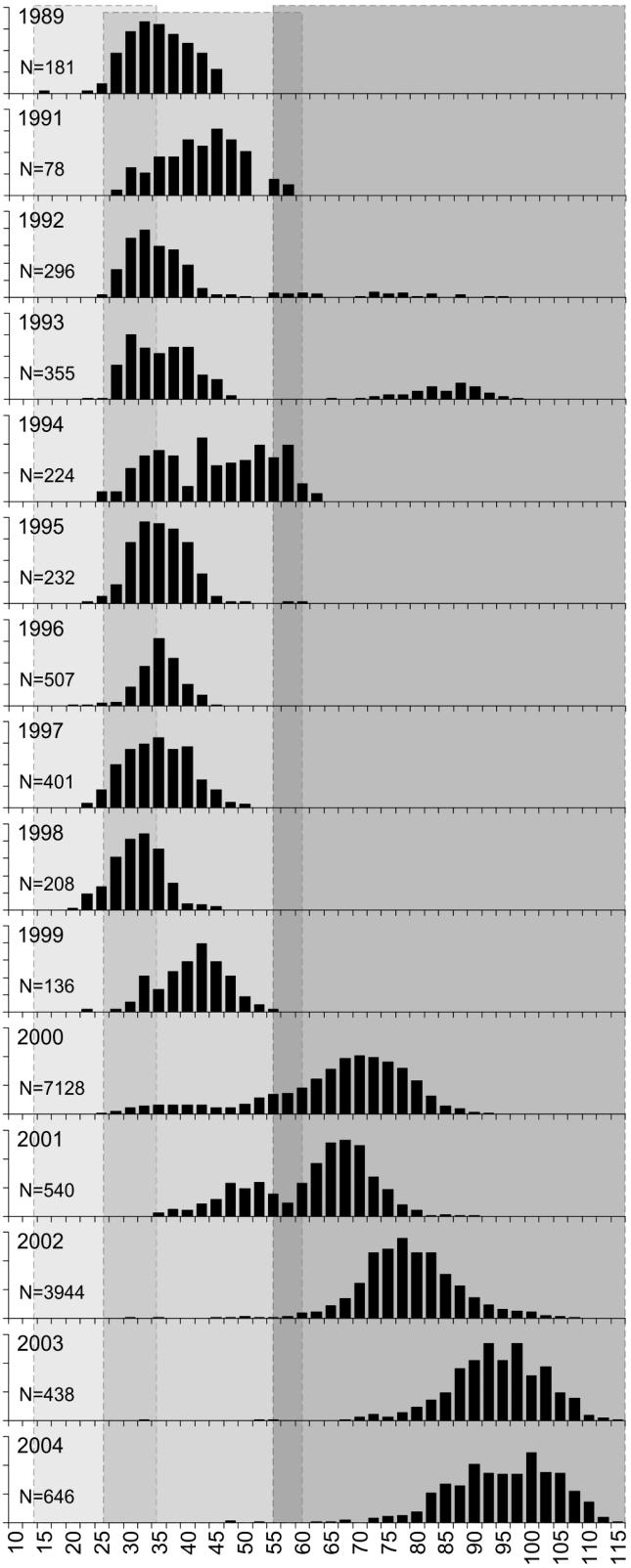

Figure 1: Occurrence of sizes (ML [cm]) of mature females by industrial jig fishery in the Peruvian EEZ; shaded boxes indicate the three groups of size-at-maturity proposed by Nigmatullin et al. (2001); modified after Argüelles et al. 2008.

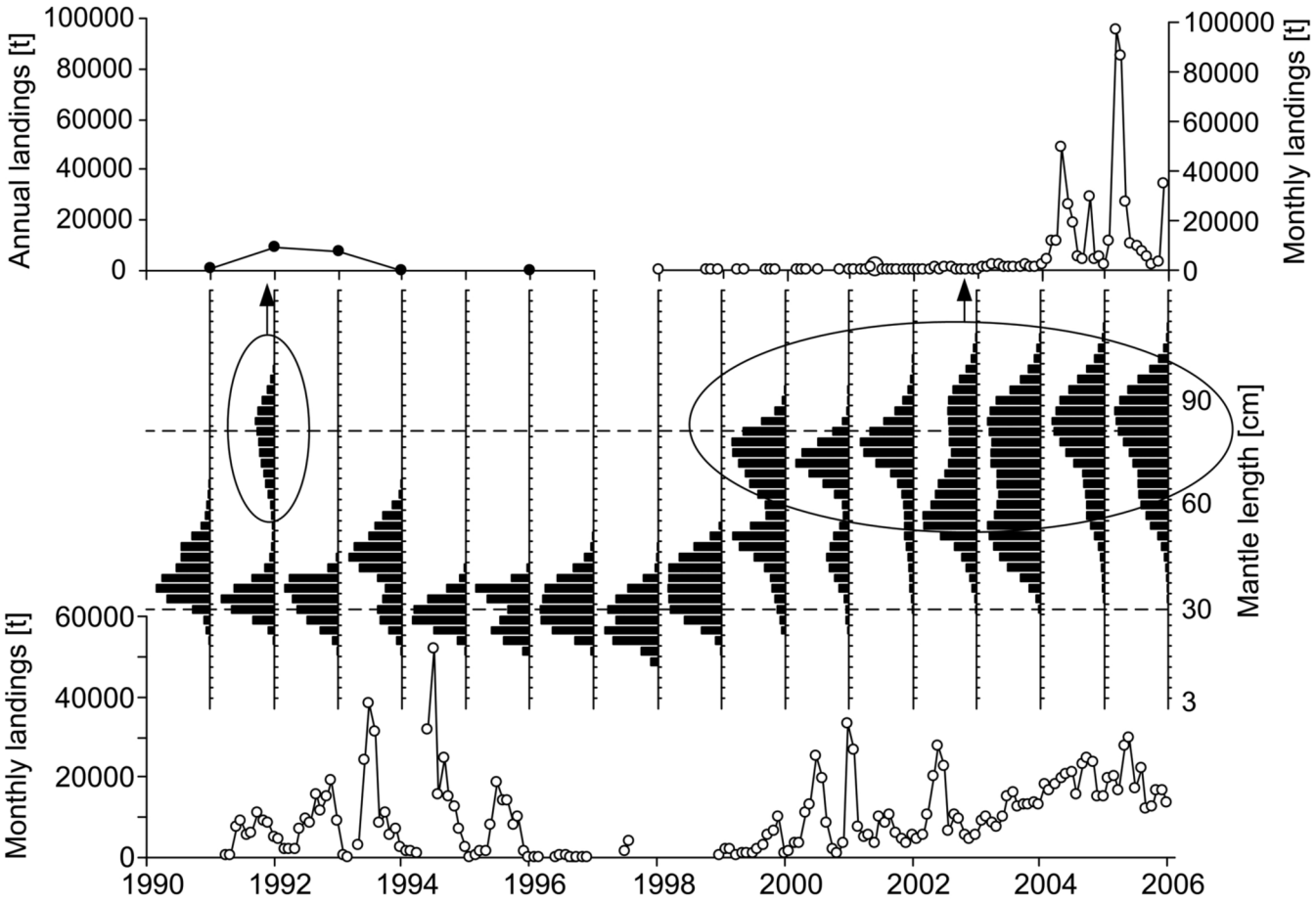

Figure 2: Temporal coincidence of high annual landings in Chilean regions IV (Coquimbo, ~30°S) to VIII (Bío-Bío, ~40°S, upper panel; filled circles: annual landings from 1991 to 97, open circles: monthly landings from 1998 to 2005) with the occurrence of the large specimen observed in the landings from the Peruvian EEZ in 1992 and from 2000 on (middle panel); lower panel: monthly landings of industrial and artisanal fishery in the Peruvian EEZ.

the number of individuals that can be reduced again by the larger individuals when the population is under ecological stress.

After the 1997–98 El Niño, a range expansion of jumbo squid was observed in the north Pacific Ocean (Zeidberg and Robison 2007; Staaf et al. 2008) and south Pacific Ocean (upper panel of fig. 2; fishery data of Chilean SENARPESCA, see web page: http://www.senarpesca.cl/). From 2002 to 2004, reported annual landings of jumbo squid from off Chile increased from 5500 t to nearly 300,000 t. This increase in landings partially resulted from the directed artisanal jig fishery for jumbo squid, but squid was mainly captured as increased bycatch of other fisheries employing different types of fishing gear (Ibáñez et al. 2008). After mass strandings in California in 2002 and sightings of *D. gigas* up to Alaska since 2002, the jumbo squid became an important target of the U.S. sport fishery (Hatfield and Hochberg 2006). This coincides with the steadily increasing biomasses as estimated from catch per unit of effort (CPUE) and acoustic surveys (IMARPE, unpubl. data) which have sustained the continuously increasing total allowable catch for the Peruvian fishery since 2000 (lower panel of fig. 2). At present, the northern and southern limits of jumbo squid distribution are 60°N and 50°S, respectively (fig. 3), although it is not clear if the expansion has ceased or will continue into new areas.

THE FUNCTIONAL TRIAD MIGRATION-MATURATION-GROWTH

Because changes in population size structure, abundance, and distribution observed during the last decade seem to be related (fig. 2), we propose that individual migration, maturation, and growth are connected via a functional triad on a physiological and energetic basis: as a mobile and fast growing hunter, *D. gigas* has a high energy demand and available food has to change rapidly in quality and size while the squid grows from the planktonic paralarva to its final length in just a few months. Migration routes must thus change with the spatio-temporal occurrence of prey items as the nutritional needs of the squid change through different size classes.

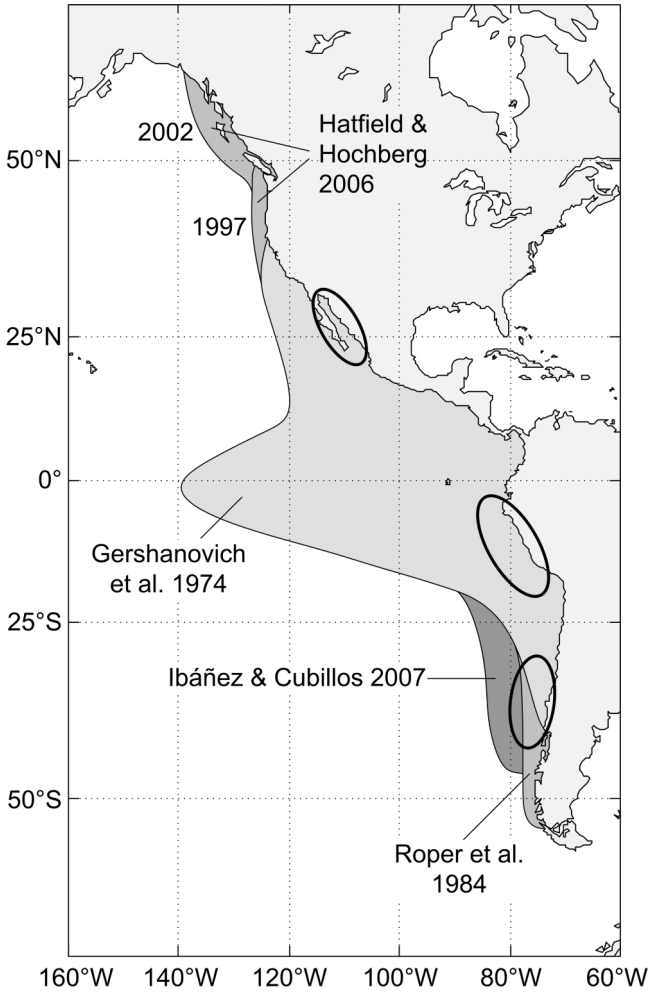

Figure 3: Distribution area of *Dosidicus gigas* according to different sources in different years indicating an extension of the range; ellipses show main fishing areas.

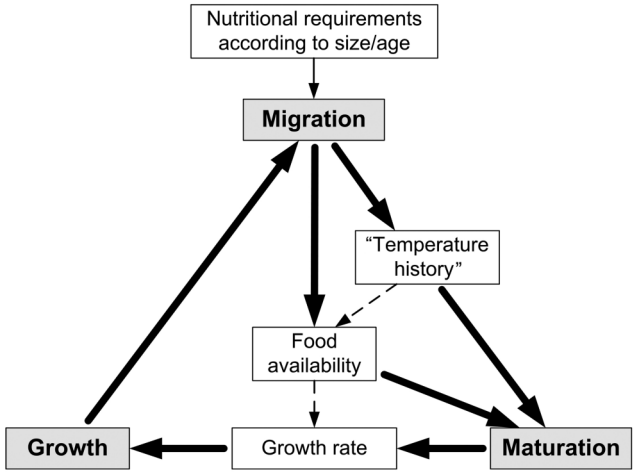

Figure 4: Scheme of the functional triad migration-maturation-growth: individual nutritional requirements lead to migration patterns that lead to a temperature history according to water masses passed, which controls the onset of maturity, that in turn controls growth rate and finally growth. Growth, i.e., the size of a specimen, again influences its migration; dashed interactions that have been reported for some cephalopod species (e.g., Pecl & Jackson 2006) have not been considered in the present hypothesis; further explanations in the text.

During the horizontal migration of up to 30 km per day (Gilly et al. 2006) and regular vertical migrations to depths of 1200 m (Nigmatullin et al. 2001), individuals pass through different water masses which leads to a unique temperature and nutrition history for each squid. We postulate that this history may govern the onset of jumbo squid maturation by a specific, but unknown, number of day-degrees, as has been suggested for other cephalopods (Rodhouse 1998). Environmental variables, temperature, and food availability have also been described as factors that control cephalopod maturation. High nutrition levels and low temperatures are known to cause late maturation and low nutrition levels and high temperatures cause early maturation (Mangold 1987). Following this reasoning, the individual temperature and nutrition history would thus determine the onset of maturation, which in turn controls the maximum size the individual can attain (fig. 4) because *D. gigas* is semelparous and dies after its first reproduction season (Nigmatullin et al. 2001). Consequently, groups of *D. gigas* that differ in size-at-maturity and final size may have experienced different environmental conditions with respect to temperature and nutrition and may have therefore migrated along different routes.

In Peruvian waters, the available data for mature females indicate that there are two size-at-maturity groups and do not support Nigmatullin et al.'s (2001) three-group hypothesis (fig. 1). The size distributions of immature and mature females and males in Peruvian landings suggest the existence of more groups in the population (fig. 2, middle panel). However, since these landings are composed of mature and immature individuals of possibly different cohorts (Tafur et al. 2001) they should not be confused with the different groups of size-at-maturity. Argüelles et al. (2001) found that individuals of the large size-at-maturity group are older than those of the small group, which agrees with our hypothesis.

Size-at-maturity groups

Very few studies have examined whether genetic, abiotic, biotic, or a mixture of these factors are responsible for observed differences in sizes-at-maturity of jumbo squid (Nesis 1983; Nigmatullin et al. 2001). This suggests that the underlying mechanism proposed in our study, which links physiological and ecological/environmental factors, has not been considered.

If, as the Peruvian fishery data suggest (figs. 1 and 2), mature specimens were divided into small/early and big/late maturing groups, the small group would be at a disadvantage since the higher *relative* energy a small in-

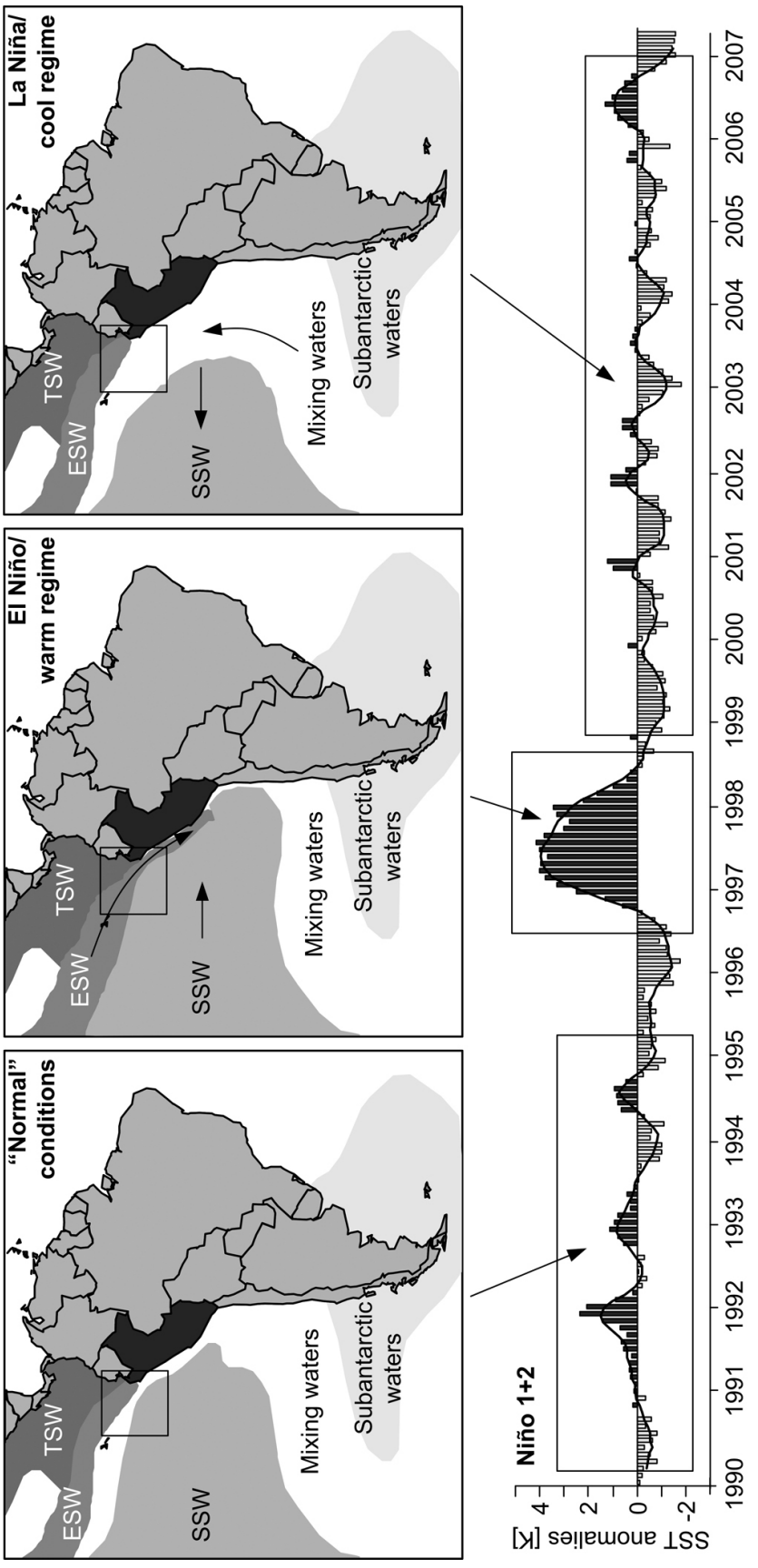

Figure 5: Schematic illustration of the "mean" location of water masses during different times/regimes in the South Eastern Pacific obtained from satellite SST data and oceanographic data collected during research and monitoring cruises of the IMARPE (after Morón and Sarmiento 1999; Ahumada et al. 2000; O. Morøn, pers. commun. IMARPE); ESW: equatorial surface waters; TSW: tropical surface waters; SSW: subtropical surface waters; the squares in the sketches show the Niño 1+2-region; lower panel shows SST-anomalies of the Niño 1+2-region.

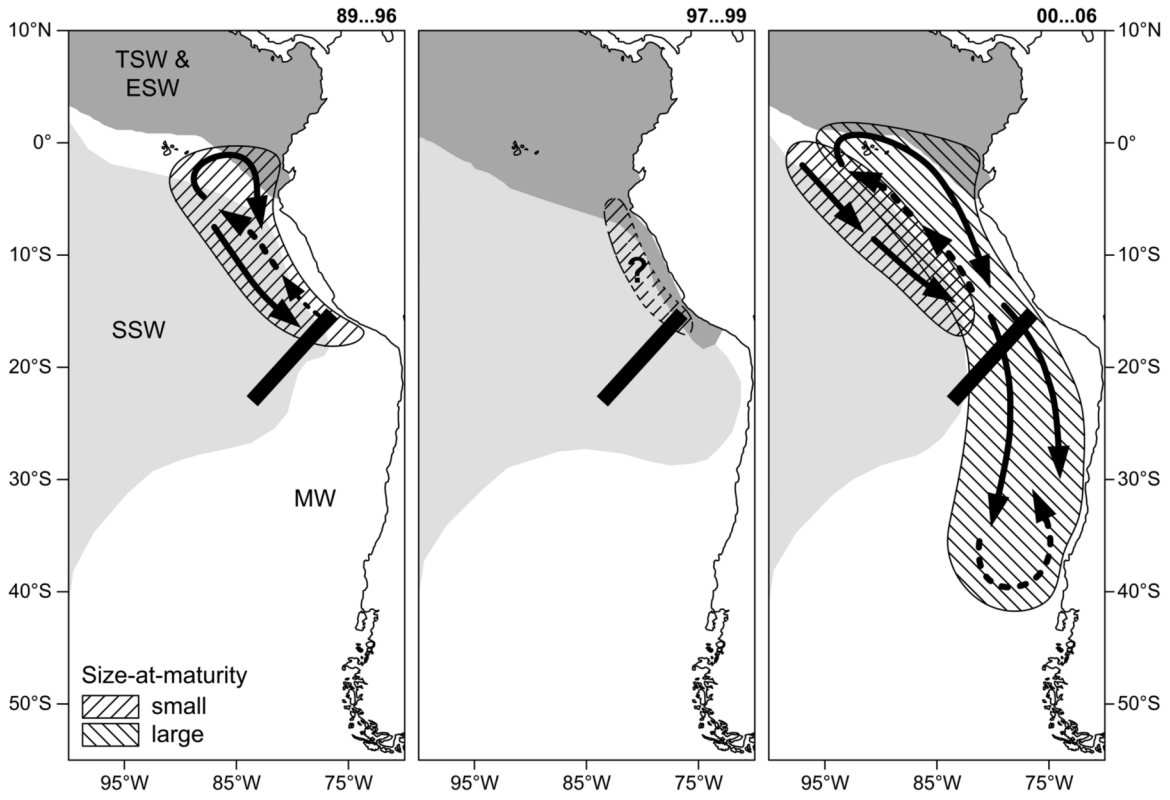

Figure 6: Scheme of distribution areas/fishing grounds and proposed migration routes of *D. gigas* in the SE Pacific during the "normal" period from 1989 to 1996, during and after El Niño 1997 to 1999 and from 2000; hatched areas: distribution areas/fishing grounds of *D. gigas*; black arrows: assumed migration patterns of *D. gigas*; broken black arrows: assumed paralarval movement; dark grey area: tropical and equatorial surface waters (TSW & ESW); light grey area: subtropical surface waters (SSW); black bars: sketch of Nazca Ridge.

dividual invests into reproduction yields a lower reproductive output (Pecl and Jackson 2006; Argüelles and Tafur 2007). Additionally, small individuals have no access to larger prey or conspecifics at higher trophic levels, as do the larger specimens. On the other hand, smaller individuals may benefit under conditions of low food availability, as individually they invest less *absolute* energy into reproduction and because they are capable of feeding on smaller, more numerous food items at lower trophic levels. An advantage of the small size-at-maturity group is also its shorter generation time, so that lower individual reproduction adds up to a high population reproduction per unit of time. Moreover, the higher population turnover rate decreases the mean trophic level of the population as small individuals predominate, allowing it to feed at the more productive lower trophic levels.

Based on the above, we propose that the two groups have opposite life-history responses to two basic ecosystem conditions of the Humboldt Current system (HCS). The small size-at-maturity strategy ensures that the population survives during warm periods with low food availability, while the big size-at-maturity strategy allows for maximizing individual fitness during cool periods with abundant prey.

Migration pattern and observed range expansion

In the HCS these conditions are related to water masses characterized by different sea surface temperatures (SST) and salinities that change their locations off the coast of Peru according to large-scale oceanographic and atmospheric conditions and the resulting intensification or weakening of currents (fig. 5). In the 1990s until the beginning of 1996, the EPO showed moderate changes between positive and negative SST anomalies, which resulted in the limit between cool mixing waters (MW) and warmer subtropical surface waters (SSW) occurring inside the Peruvian EEZ. During the strong El Niño of 1997–98 the equatorial undercurrent (EUC) increased in strength, transported very warm equatorial surface waters southward, pushed the SSW closer to the Peruvian coast, and weakened the highly productive coastal upwelling cells. From 1999 on, a general cool regime entered the eastern Pacific Ocean, characterized by intense upwelling, a strong Humboldt Current and weak EUC. It produced negative SST anomalies in the Peruvian EEZ by pushing the limiting SSW farther westward and outside the Peruvian EEZ, and by allowing the formation of a broad zone of cool, nutrient-rich MW off the Peruvian coast

(Morón and Sarmiento 1999; O. Morón, pers. commun. IMARPE).

We assume that changes in water mass distributions lead to changes in the distribution area and main fishing grounds of *D. gigas* (fig. 6). The small size-at-maturity group found in the official landings data for the early 1990s is assumed to be associated with the boundary between the cool MW and warmer SSW and to move back and forth between the two water masses. Migration to the southern part of the HCS during that period seems to be restricted to some years and a low number of individuals. Although exact mechanisms are not known, this may result from the location of the SSW relative to the Nazca Ridge (black bars in fig. 6) that possibly acts as a barrier for smaller *D. gigas*, preventing them from migrating to colder waters in the south. This barrier may have its origin in bathymetric and oceanographic conditions different from those farther south and farther north off the Peruvian coast (Wolff et al. 2003; Shaffer et al. 2004), leading to significantly weaker upwelling and to less productivity in coastal areas farther south (Longhurst 1995).

Further evidence for this is found in the data from the industrial fishery inside the Peruvian EEZ which indicate that the resource is mainly distributed north of the Nazca Ridge (Taipe et al. 2001). With DMSP-OLS images it is possible to assess night-time activities of the industrial jumbo squid jigging fleets as they use strong lights to attract their target (Waluda et al. 2004). A night-time light image integrating the cloud-free nights in 2003 (fig. 7) shows that just south of the Nazca Ridge no jig fishery has occurred this year.

Since 1999, the size of the individuals in the landings reported to Peruvian authorities increased due to the displacement of the limit of the two water masses farther offshore and outside the Peruvian EEZ (fig. 5). Inside the Peruvian EEZ the cool, nutrient-rich MW were found, and with these the big size-at-maturity group developed that was reported to national Peruvian fishery authorities. Since then, the limit between the warmer SSW and the cooler MW has been outside the 200-mile border and, according to our hypothesis, the small size-at-maturity group should be found there. Night-time satellite images suggest that the international jigging fleet has been operating outside the EEZ at all times (Waluda et al. 2004; IMARPE, unpubl. data) but no data on catches and population structure are available. Preliminary investigations of more recent night-time images at IMARPE and the night-time lights image of 2003 (fig. 7) suggest that the bigger part of the total industrial fishing effort is applied outside the EEZ.

Preliminary results from IMARPE's October–November 2007 research cruise, 0710–11, support this hypothesis. During the survey that covered the east-west trajectory from 30 nm to 350 nm off the northern Peruvian coast (4°S to 8°S), all mature individuals (72 to 98 cm ML; $n = 5$) fished by trawl net and manual jigging inside the EEZ belonged to the large size-at-maturity group, and those outside it (22 to 42 cm ML; $n = 18$) to the small group. This suggests that the large size-at-maturity group occurs mostly inside the EEZ and the small size-at-maturity group outside the EEZ because of the new water mass distribution. We propose that larger animals are restricted from reaching the warmer waters now found outside the EEZ because they require higher nutrition levels than these waters can provide. Individuals of the small group moving to cooler water masses inside the EEZ become part of the large size-at-maturity group as a consequence of the conditions of their new environment. This leads to a separation of the

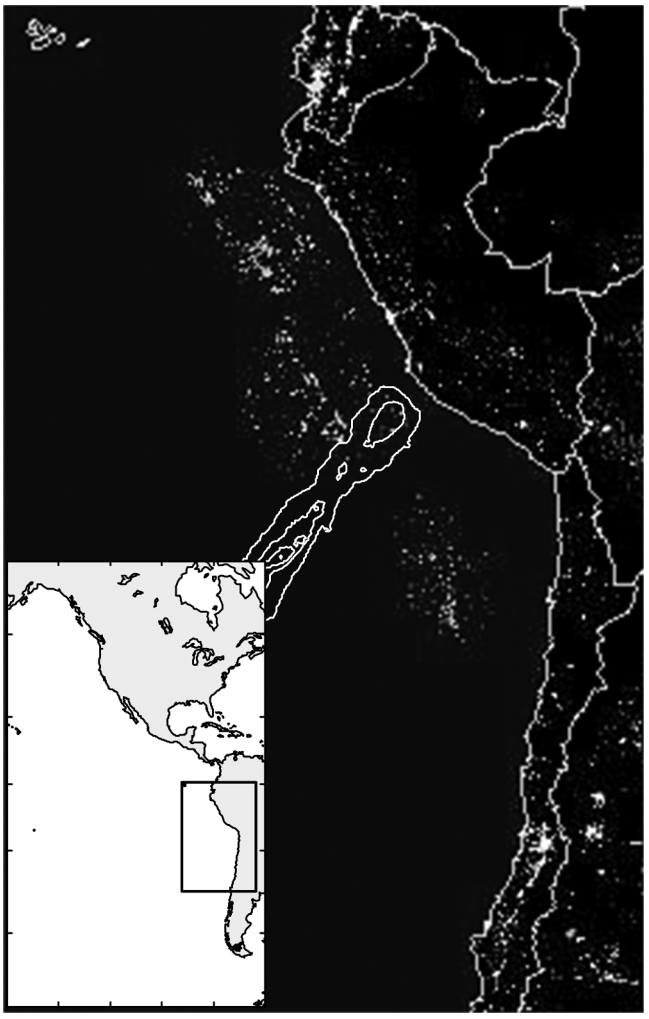

Figure 7: Integrated nighttime lights image of 2003 basing on visible and infrared radiation satellite data; white points off Peru and Chile indicate lights employed during nighttime fishing activity of the industrial jig fishery (modified after National Geophysical Data Center; http://www.ngdc.noaa.gov/dmsp/); Nazca Ridge is shown by depth lines in 1000 m intervals.

two size-groups that helps small individuals avoid falling prey to larger conspecifics.

The barrier formed by the Nazca Ridge and the water-masses ceases to exist with the retraction of the SSW from the coast, enabling parts of the population to migrate upstream along the Humboldt Current to Chilean waters. In the area from 30°S to 40°S where the Humboldt Current departs from the Chilean coast, they become vulnerable to fisheries again and are caught in large quantities. Clarke and Paliza (2002) proposed that mature jumbo squid may spawn in this area, but to our knowledge no one has yet reported paralarvae in Chilean waters. It is unknown whether spawning occurs in this area, or if the same individuals return to warmer waters off Peru to spawn, or die without spawning. However, periodic mass strandings in southern Chile have been reported (Ibáñez and Cubillos 2007). Few jumbo squid are fished in waters off northern Chile inside the EEZ (SENARPESCA data), however, in 2003 the international jigging fleet operated outside the EEZ (fig. 7). Again, the exact reason for this remains unclear but may result from the environmental conditions mentioned before. The changing intensities of the oceanic and a coastal branch of the northward flowing Humboldt Current in this area in different periods (Blanco et al. 2002) may also contribute to the observed distribution patterns.

RANGE EXPANSION OF *D. GIGAS*: WHY NOW?

Although jumbo squid have never before been sighted as far north as Alaska, nor has the Chilean fishery reported such high landings since 2003, range expansions have been observed before in both hemispheres (Hatfield and Hochberg 2006; Ibáñez and Cubillos 2007; Staaf et al. 2008). Thus the question arises: why is the present range expansion so much stronger? We assume that both environmental variability and the indirect effect of fishery pressure in the HCS and the CCS affect the range expansion.

The last decade has seen a rare succession of environmental phenomena: after the strong La Niña/El Niño combination from 1996 to 1998, a Pacific-wide regime shift from warm to cool occurred that can be observed in the SST-anomalies off Peru (lower panel of fig. 5). The La Niña/El Niño period is considered as a "system reset" that can allow rapidly reproducing species to move into environmental "loopholes," i.e., niches formerly occupied by other species (Bakun and Broad 2003). The "loopholes" in the EPO open after the La Niña/El Niño-"system reset" and are exceptionally accessible for *D. gigas* because cool-regime waters are nutrient rich. At the same time, fisheries have greatly reduced the abundance of *D. gigas* competitors, such as mackerels and hake, and predators, like sharks and marine mammals (Tam et al. 2008), in the last decades (Pauly and Palomares 2005; Lotze et al. 2008), but have probably not affected their prey as euphausiids and myctophids.

These have been found to be important in the diet of *D. gigas* in the CCS (Markaida et al. 2006a) and the HCS (Blasković et al. 2007; Taylor et al. 2008) and can rapidly build up vast biomasses. No exploitation of the most important myctophid in the HCS, *Vinciguerria lucetia*, is known (Froese and Pauly 2007), and there are no reports of human exploitation of euphausiids in the HCS. The biomass increase of *V. lucetia* since 2000 may have partially fueled the increased biomass of jumbo squid (fig. 8, IMARPE, unpubl. data). Pauly et al. (2002) suggested that the abundance of marine resources such as invertebrates and jellyfish have a strong positive response to fishery-caused reductions in their competitors and predators. These groups are fast growing species often considered suppressed under "normal" conditions.

Thus, it seems that the concurrence of favorable "loopholes" after a "system reset" and fishery-caused reductions in competitors and predators has enabled *D. gigas* to expand its range.

CONCLUSION AND FINAL REMARKS

The proposed migration-maturation-growth triad can explain the observed changes in population structure, abundance, and distribution of jumbo squid in the eastern Pacific Ocean during the last decade. Direct experimental evidence to prove our hypothesis is still missing, however. Until now it has not been possible to keep *D. gigas* under controlled aquarium conditions and the longest reported period that an adult jumbo squid has survived in captivity is 12 days (Gilly, Hopkins Marine Station, pers. comm.); paralarvae have been reported to survive 10 days (Ichii et al. 2002). Nevertheless, experimental work in the laboratory should be conducted to verify—or falsify—that *D. gigas* maturation and growth depend on temperature and food, which Mangold (1987) suggests for cephalopods in general. Other support for the hypothesis could come from biometric and maturity data from the Japanese and Korean jumbo squid fisheries, believed to have been operating outside the Peruvian EEZ for as long as those operating inside.

We have concentrated our analysis on the Peruvian part of the HCS, and further studies should clarify if the proposed triad also explains the range expansion and change in population size structure of *D. gigas* in the Gulf of California and the Californian Current system of the northern hemisphere, which are subjected to similar environmental and—at least in the Gulf of California—fishery conditions.

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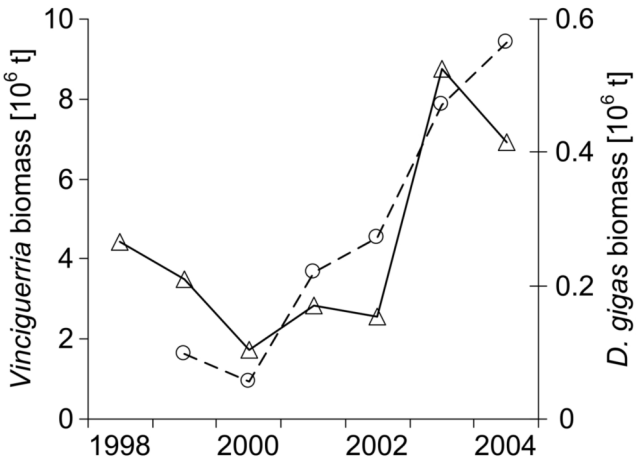

Figure 8: Biomasses of the myctophid *Vinciguerria* (triangles) and *D. gigas* (circles) in the Peruvian EEZ (IMARPE data from acoustic surveys).

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INTERACTIONS BETWEEN JUMBO SQUID (*DOSIDICUS GIGAS*) AND PACIFIC HAKE (*MERLUCCIUS PRODUCTUS*) IN THE NORTHERN CALIFORNIA CURRENT IN 2007

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ABSTRACT

During a joint Canada-U.S. Pacific hake (*Merluccius productus*) acoustic-trawl survey in 2007, 82 jumbo squid (*Dosidicus gigas*) were captured at depths exceeding 300 m offshore of the continental shelf along Vancouver Island and the Queen Charlotte Islands. Because the acoustic signs associated with these captures were unusual, we compared 38 kHz echograms collected during trawls in which both hake and jumbo squid were caught with those from nearby trawls in which only hake or squid were caught. Hake appeared to be more widely dispersed or less densely aggregated when jumbo squid were captured concurrently. We hypothesize that squid predation causes an avoidance response in hake, thereby altering normal aggregation behavior. Although our evidence of jumbo squid predation on Pacific hake is limited to seven echogram comparisons, this new predator-prey interaction may lead to cascading trophic impacts in the northern California Current. On a practical level, our findings also suggest that the acoustic survey methods, which use a combination of visual echogram interpretation and trawling to verify target identification, will require adjustment. If hake are dispersed over larger coastal areas or do not aggregate as recognizable targets when jumbo squid are present, then additional ship time and other resources may be required for future acoustic-trawl surveys.

INTRODUCTION

Jumbo squid (*Dosidicus gigas*) were first sighted in northern California Current waters off Oregon in 1997 (Pearcy 2002) and in waters off Washington and British Columbia in 2004 (Cosgrove 2005; Trudel et al. 2006). Between 2002 and 2006, jumbo squid underwent a rapid range expansion from eastern tropical Pacific waters into the southern California Current (Field et al. 2007) that coincided with climate-related increases in regional sea surface temperature and declines in large predatory fish that prey on squid (e.g., Field et al. 2007; Zeidberg and Robison 2007). Local declines in Pacific hake (*Merluccius productus*) abundance in Monterey Bay between 1998 and 2005 (Zeidberg and Robison 2007) and Chilean hake (*M. gayi*) abundance off central Chile between 2000 and 2007 (Arancibia and Neira[1]) may be related to increased jumbo squid predation as a result of range expansion (e.g., Field et al. 2007) or to shifts in hake distribution driven by climate-related changes in sea surface temperature (e.g., Smith et al. 1990).

Pacific hake is the most abundant groundfish in the California Current system and is an important commercial species in both Canada and the United States (Ressler et al. 2007). The coastal or offshore Pacific hake stock (referred to as hake hereafter) is the largest and most important of three stocks along the west coast of North America. This stock disperses from winter spawning grounds off southern California to northern feeding areas off the coasts of northern California, Oregon, Washington, and British Columbia during the summer months (June through August) where it forms dense midwater aggregations at depths of 150–300 m along the continental shelf break during daylight hours (Dorn 1995; Mackas et al. 1997).

Echo-integration trawl surveys (acoustic surveys) to assess the distribution and abundance of hake have been conducted since 1977 jointly by the United States National Marine Fisheries Service with Canada's Department of Fisheries and Oceans since 1992, under the auspices of the International Hake Treaty which recognizes that this stock is a transboundary resource. These surveys are conducted between June and September and target aggregations of adult hake (age 3 and older) along the continental shelf and upper slope from central California (36°N) to Dixon Entrance, British Columbia (54.7°N), or southeast Alaska, if necessary (fig. 1). Survey timing coincides with the completion of the annual northward migration and the full availability of hake to the survey (Nelson and Dark 1985). Acoustic backscatter data at 38 kHz attributed to hake are converted into estimates of biomass and abundance and verified using data from midwater and bottom trawls that confirm species composition and provide measurements of length,

[1]Arancibia, H., and S. Neira. 2007. An overview of the present state of common hake (*Merluccius gayi*) stock with a forecast of its biomass including jumbo squid (*Dosidicus gigas*) prey-predator relationship in central Chile (33°S–39°S). Paper S-7 presented at California Cooperative Oceanic Fisheries Investigations Annual Science Conference 2007, Hubbs-SeaWorld Research Institute, San Diego, California, November 26–28, 2007.

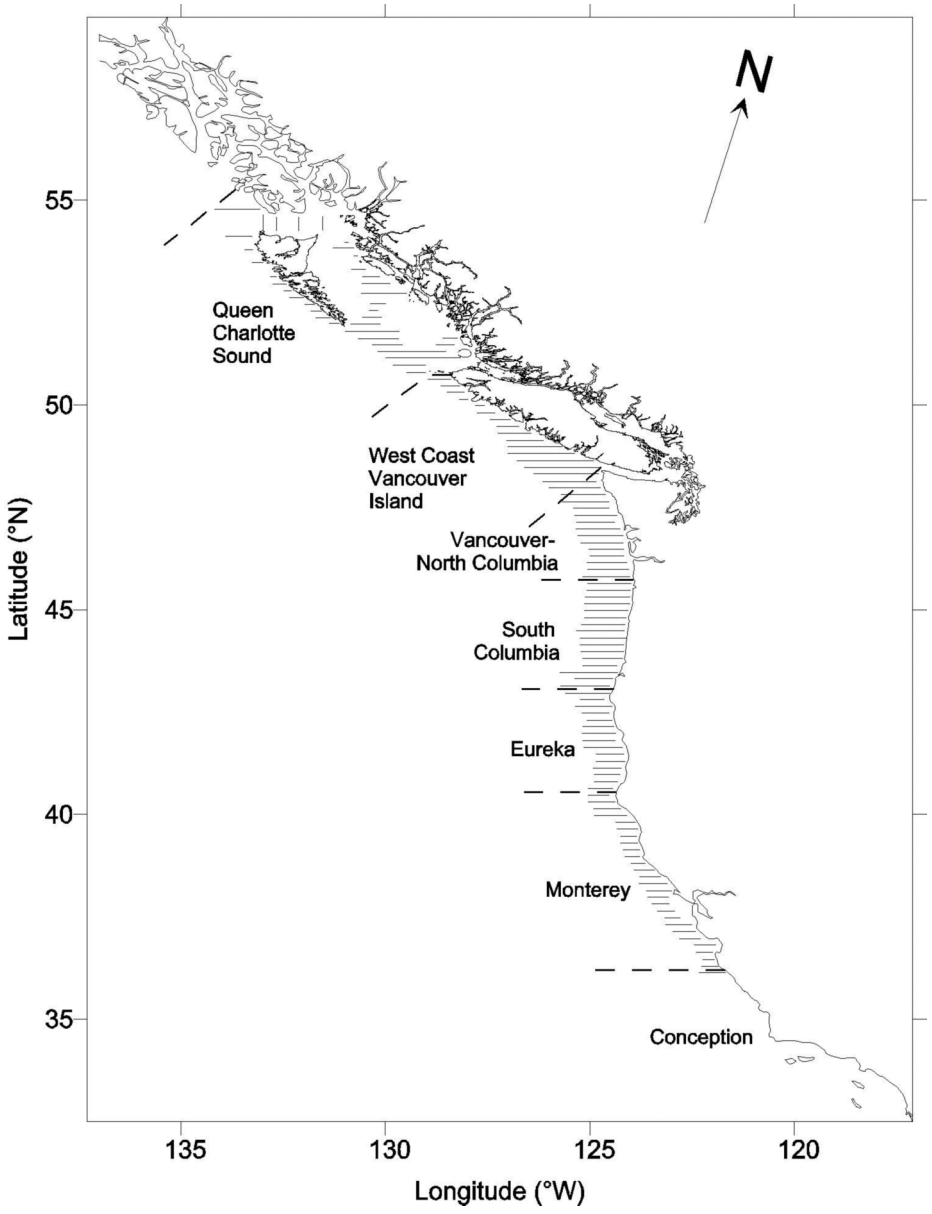

Figure 1. Generalized Pacific hake (*Merluccius productus*) acoustic survey transect pattern along the west coast of North America. Latitudinal location of transects in each survey may vary from those shown since placement is measured in 10 nmi intervals from a randomly chosen starting latitude south of Monterey, California. Statistical areas are from the International North Pacific Fishery Commission, with modifications in Canadian waters, and are used to group hake backscatter data for analysis.

weight, sex, and age. The acoustic surveys were conducted triennially between 1977 and 2001 and biennially from 2001 to 2007. The protocols and methodology used in these surveys are consistent with the best practices used worldwide (MacLennan and Simmonds 1992) and are fully described by Guttormsen et al. (2003) and Fleischer et al. (2005).

The earliest confirmed incidental catches of jumbo squid in the acoustic survey time-series (1977–2007) occurred in 2003 (Fleischer et al. 2005), although a specimen, lost before the Royal British Columbia Museum could confirm identification, was caught during the 1998 survey (K. Cooke, Fisheries and Oceans Canada, pers. comm.). Several authors have suggested that the recent range expansion of jumbo squid in the eastern Pacific Ocean may result in increased predation on hake (e.g., Field et al. 2007; Zeidberg and Robison 2007) and this predation combined with high fishing mortality will mean that hake are unlikely to be effective competitors with jumbo squid (Rodhouse 2008). In this paper, we document jumbo squid catches during hake acoustic surveys conducted between 2001 and 2007. We focus on

2007 sightings because unusual acoustic signs recorded during this survey led us to hypothesize that interactions between jumbo squid and hake were affecting normal hake aggregation behavior.

METHODS

Our data sets consist of trawl catch data and acoustic backscatter data per unit area (s_A– m^2/nmi^2) collected during acoustic surveys of hake in 2001, 2003, 2005, and 2007. The trawl data set consists of numbers and total weights (kg) of all recognizable species as well as length, sex, maturity, and condition data for hake. Raw acoustic data from Simrad 38 kHz and 120 kHz split-beam transducers in the 2001 and 2003 surveys and Simrad 18, 38, 120, and 200 kHz split-beam transducers in the 2005 and 2007 surveys were logged, but the 38 kHz acoustic signals are the primary data source for quantitative hake acoustic backscatter (s_A) measurements. Data from other frequencies were used qualitatively as aids in determining hake water column distributions.

Acoustic data were collected with Simrad EK500 (2001, 2003) or EK60 (2005, 2007) scientific echosounding systems. The transducers were located on a hydraulic ram that was extended 1.2 m below the keel to 5.2 m below the surface (CCGS *W. E. Ricker*) or on a centerboard that held the transducers 9 m below the surface (NOAA RV *Miller Freeman*). Acoustic sample rates were automatically determined based on sound propagation and internal processing constraints, but ping intervals typically ranged from 0.5 s in shallow waters to 2.5 s at water column depths >1000 m. The acoustic systems were calibrated in the field before, sometimes during, and after the survey by suspending copper spheres with known backscattering cross-sections below the transducers and measuring the acoustic returns using standard procedures described by Foote et al. (1987) and MacLennan and Simmonds (1992). Split-beam target strength and echo-integration data were collected to calculate echosounder gain parameters and beam patterns during calibration.

Acoustic data (s_A) were collected along east-west oriented transects spaced at 18.5 km (10 nautical miles) intervals from a randomly chosen starting latitude south of Monterey, California (fig. 1). The inshore and offshore ends of each line were established when hake were no longer detectable acoustically or, in the absence of hake, from 50 m depth inshore to 1500 m depth offshore. Both the southern and northern limits of the survey grid were initially based on historical knowledge of hake distribution patterns and environmental conditions prior to a survey. Near real-time satellite data on coastal ocean conditions and commercial fishing reports were reviewed at sea to ensure that survey coverage encompassed the full expanse of the hake distribution at the time of each survey. Acoustic data were collected at vessel speeds of 9–12 knots (4.6–6.1 m/s) and only during the day when hake were acoustically detectable and aggregations recognizable on the echogram. Shortly after sunset and throughout the night, hake disperse in the water column, mixing with other species and reforming in discrete layers around sunrise (Guttormsen et al. 2003; Fleischer et al. 2005).

Midwater and bottom trawls were used to obtain representative catches of species composition and size distributions of organisms detected acoustically. Trawls were conducted based on the occurrence and pattern of backscattering layers observed at the time of each survey rather than using a sampling design with predetermined locations and effort. Distinct layers of intense backscatter consistent with high densities of hake were the highest priority for trawl sampling, but other types of backscattering features, both in terms of marginal areas

TABLE 1
Summary of integrated acoustic and trawl surveys conducted jointly by Canada and the United States since 2001.

	2001[a]	2003	2005	2007
Vessel	*Miller Freeman: W.E. Ricker*	*W.E. Ricker*	*Miller Freeman*	*Miller Freeman*
Survey dates	15 June–29 July, 6–18 August	29 June–01 September	20 June–19 August	19 June–21 August
Start–end latitudes (°N)	36.2–50.2; 50.2–54.8	36.1–51.4	35.7–54.8	35.8–54.8
Acoustic frequencies (kHz)	38, 120	38, 120	18, 38, 120, 200	18, 38, 120, 200
Vessel speed (m/s)	6.0; 4.6	4.6–5.1	5.6–6.1	5.6–6.1
Number of transect lines	81; 49	115	106	133
Total survey distance (km)	4,870; 640	6,756	21,246	21,201
Trawl Gear[b] (Number of trawls)	AWT (72), PNE (14), PRT (41)	PRT (88), PYT (18)	AWT (61), PNE (2)	AWT (82), PNE (10)
Biomass estimate (x 10^6 t)	0.74	1.84	1.26	0.88
% biomass—Canada	10	20.3	40.4	25.3
% biomass—United States	90	79.7	59.6	74.7
Reference	Guttormsen et al. (2003)	Fleischer et al. (2005)	Fleischer et al. unpubl. ms[c]	

[a]Order of column values is RV *Miller Freeman* followed by CCGS *W.E. Ricker*; both ships used the same acoustic frequencies.
[b]AWT—Aleutian wing midwater trawl with a codend of 3.2 cm; PNE—polyethylene Nor'eastern bottom trawl with a 3.2 cm codend mesh liner; PRT—Polish rope midwater trawl with 1 cm codend mesh; PYT—Poly-Yankee 36 bottom trawl with 2.5 cm codend liner.
[c]Fleischer, G. W., K. D. Cooke, P. H. Ressler, R. E. Thomas, S. K. de Blois, and L. C. Hufnagle. In prep. The 2005 integrated acoustic and trawl survey of Pacific hake, *Merluccius productus*, in U.S. and Canadian waters off the Pacific coast. U.S. Dept. Comm., NOAA Tech. Memo.

TABLE 2
Aquatic species accounting for ≥90% of biomass in pelagic and bottom trawls during hake echo-integration trawl surveys, 2001–2007. Figures are proportion of total catch weight in each survey. Data taken from Guttormsen et al. (2003), Fleischer et al. (2005), and Fleischer et al.[a]

	2001		2003		2005		2007	
Species	Pelagic	Bottom	Pelagic	Bottom	Pelagic	Bottom	Pelagic	Bottom
Pacific hake	66.9	60.1	78.6	72.7	86.9	56.1	91.4	
Pacific herring	10.6		3.4					
walleye pollock	8.8			1.6				
spiny dogfish	3.9	0.9	6.7		1.0	37.8	1.2	
canary rockfish							1.8	
splitnose rockfish		15.1		3.3	3.3			
yellowtail rockfish	6.1		1.0		2.7		2.9	
widow rockfish					1.7			
yellowmouth rockfish			4.0		1.1			
Pacific ocean perch		10.8	1.2	2.4	1.1			
chillipepper rockfish			1.6	2.1				
silvergray rockfish				2.5				
sharpchin rockfish		2.7						
redstripe rockfish		1.2						
stripetail rockfish				1.7				
Pacific sanddab		1.8						
arrowtooth flounder				1.9				
rex sole				1.1				
Dover sole		1.2		1.7				
jumbo squid	0	0	0.4	0	<0.1	0	1.0	

[a]Fleischer, G. W., K. D. Cooke, P. H. Ressler, R. E. Thomas, S. K. de Blois, and L. C. Hufnagle. In prep. The 2005 integrated acoustic and trawl survey of Pacific hake, *Merluccius productus*, in U.S. and Canadian waters off the Pacific coast. U.S. Dept. Comm., NOAA Tech. Memo.

of low fish density and putative aggregations of species other than hake, were also sampled (Fleischer et al. 2005). Because the trawls targeted hake for verification of acoustic sign and because tow effort and locations were not standardized between surveys, neither relative nor absolute abundances of incidental species can be inferred from the trawl data.

Research vessels and trawl gear used for surveying hake varied with survey year, although the majority of effort and catches were with midwater trawls (tab. 1). Either a Polish rope trawl (PRT) with 20 m vertical opening and 1 cm codend mesh (CCGS *W. E. Ricker*) or an Aleutian wing trawl (AWT) fitted with a 3.2 cm or 1.2 cm codend mesh liner (NOAA RV *Miller Freeman*) were used for midwater and near-bottom sampling. Bottom trawls were made using a Poly-Yankee 36 research trawl (PYR) with a 4–5 m vertical opening, roller gear on the footrope, and a 2.5 cm codend mesh liner (CCGS *W.E. Ricker*) or with a polyethylene Nor'eastern (PNE) high opening bottom trawl (NOAA RV *Miller Freeman*) fitted with roller gear and a 3.2 cm codend mesh liner (Guttormsen et al. 2003). We compiled data on jumbo squid catches and locations from all surveys, beginning with the 2001 survey. Echograms were catalogued (S. de Blois, U.S. National Marine Fisheries Service, Seattle, Washington, unpubl. data) to illustrate characteristic backscatter patterns for targets verified with trawl catches during the 2005 and 2007 surveys. Using the results from the 2007 survey, we visually compared and contrasted 38 kHz echograms at locations with catches of both hake and jumbo squid and echograms at nearby locations in which trawl catches were dominated by hake alone.

RESULTS

Pacific hake were the dominant species by weight in both pelagic and bottom trawl catches (tab. 2), consistent with the targeted approach to trawling for acoustic sign verification during the acoustic surveys. Spiny dogfish (*Squalus acanthias*) and a variety of rockfish species (*Sebastes* spp.) were the most common incidental species in these catches. Incidental catches of rockfish are not unusual since trawling is often conducted in areas where hake and rockfish are known to mix (e.g., northwest tip of Vancouver Island) in order to assign proportions to the mixed acoustic signal for species-specific biomass estimates. The first verified catches of jumbo squid in the acoustic survey time-series (1977–2007) occurred in two trawls near San Francisco in 2003 at depths of 317 and 434 m (tab. 2; fig. 2). The number of squid caught in hake trawls increased from 67 (66 in a single tow) in 2003 to 82 from seven tows in 2007. Total trawl effort (the number of trawls regardless of the length of the tow) was 106, 63, and 92 in the 2003, 2005, and 2007 surveys, respectively (fig. 3). The low catch of only three jumbo squid in three tows in 2005 does not necessarily reflect squid dynamics since operational constraints reduced overall trawling effort during this survey. The aver-

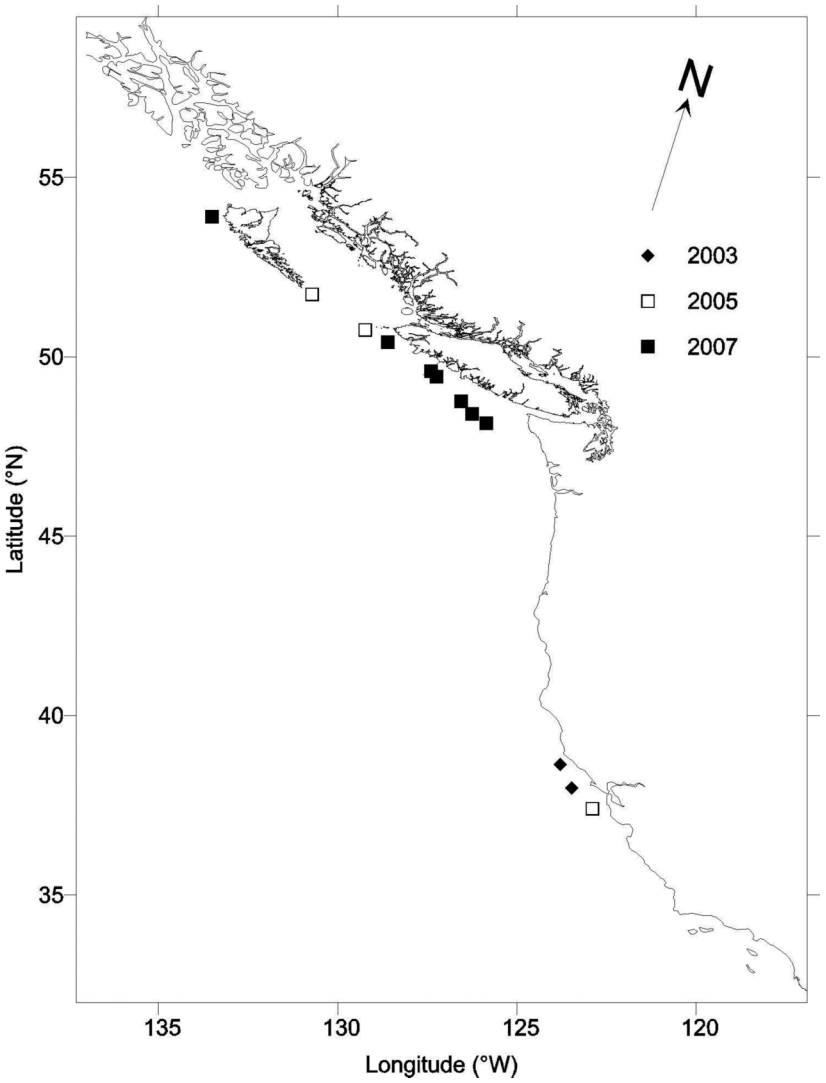

Figure 2. Jumbo squid (*Dosidicus gigas*) catch locations during 2003, 2005, and 2007 hake (*Merluccius productus*) acoustic surveys of the Pacific coast of North America.

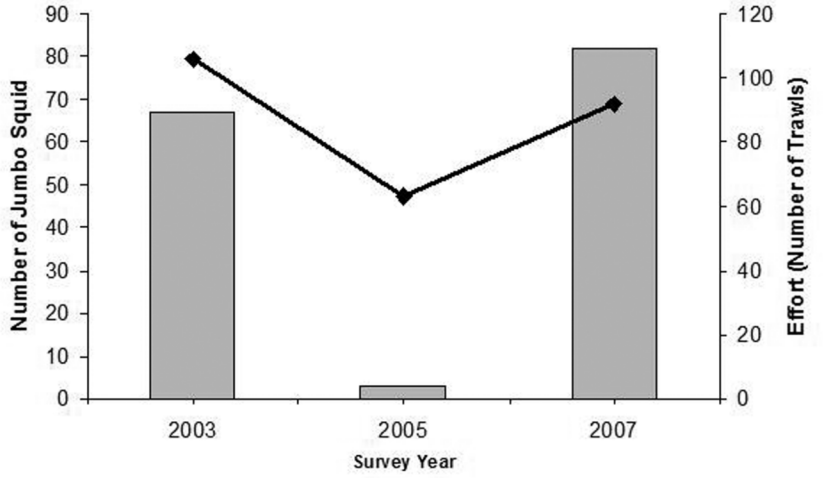

Figure 3. Total jumbo squid (*Dosidicus gigas*) catches (bars, left axis) and trawl effort (line, right axis) during 2003, 2005, and 2007 hake (*Merluccius productus*) acoustic surveys of the Pacific coast of North America.

age size of captured squid was similar in all years (5.4 kg in 2003, 5.0 kg in 2005, 5.7 kg in 2007). Jumbo squid were captured with hake in seven pelagic trawls north of 48°N in 2007 (fig. 2) and west of the shelf break at an average depth of 366 m (ranging from 330-400 m). One midwater tow in 2007 (Transect 75, the most southern 2007 location shown in fig. 2) captured jumbo squid at a depth of 400 m but no hake. The majority of recent jumbo squid catches (84 of 85 in 2005 and 2007 combined) were north of 48°N (fig. 2) at depths ranging from 172 to 405 m, at or west of the continental shelf break (defined as the 200 m isobath).

Since our analysis in this paper relies on echogram interpretation, we provide a brief description of echograms and their contents. An echogram displays the location of backscatter (targets) in the water column with respect to depth below the transducer vertically, and distance travelled by a survey vessel horizontally. A depth grid at 50 m intervals and a distance grid at 0.5 nmi intervals are overlaid on the echogram to facilitate orientation and interpretation. The choice of vertical and horizontal intervals is arbitrary and can be changed to suit different users. The spacing of the distance grid (vertical lines in the echograms that follow) is constant when vessel speed is constant, but will change when the vessel slows (wider) or increases (narrower) speed. The strongest echoes are returned by the bottom, which typically appears as a heavy dark trace overlaid with a lighter bottom tracking line produced by the echosounder (and referred to as the sounder-detected bottom). When water depth is shallow (<200 m) and the bottom is composed of hard substrates, second and third bottom echoes will appear below the first or true bottom echo (see figs. 4A, 5B, 6B for examples of multiple bottom echoes). Echoes above the bottom trace represent targets (plankton, fish) in the water column. Fish and plankton are identified by the visual pattern of these echoes, their location in the water column relative to bottom features, and the intensity and density of echoes at different frequencies (higher frequencies detect smaller organisms such as plankton, lower frequencies are better at detecting larger organisms, such as fish) combined with trawl sampling to verify user interpretations. Echograms display echo intensity on a logarithmic scale (dB) using a color scheme derived by Simrad (1993) for the EK500 echosounder, which represents low echo intensity with "cold" colors (green, blue, grey) and high echo intensity with "warm" colors (yellow, orange, red). We produced the echograms in this paper as grey-scale images (figs. 4–6), but the original color images are available from the authors by request. In the echograms that follow, echo intensity is displayed on a grey scale, with light to moderately-dark greys corresponding to low s_A in the water column (low fish density) and dark grey to black corresponding to high s_A in the water column (high fish density). Areas with no echo returns, or where acoustic signal intensity falls below a minimum threshold of –69 dB, are white. The threshold is used to remove acoustic noise and echoes from organisms too small to be hake. The bottom appears as a broad grey zone outlined with a lighter grey trace line that follows the bathymetry and represents the sounder-detected bottom.

Hake show two distinctive visual patterns on the 38 kHz echogram at normal vessel survey speeds during the day in the vicinity of the shelf break based on signal intensity, morphological criteria, and relative density in the water column. A low-density pattern consists of a diffuse speckled band of small grey groups or layers of fish spread over a broad depth range as on Transect 55 in 2007 (grey regions outlined by polygons in fig. 4A). This low-density scatter often includes other small meso-pelagic fishes such as Myctophidae (lanternfishes) and plankton (light grey targets underlying the polygons in fig. 4A). Conversely, high densities of hake produce distinct clusters (schools) or a W-shaped band of darker grey tones and black that may continue relatively unbroken for distances up to several kilometers (dark grey patterns in polygon in fig. 4B). The high-density patterns generally span a narrower depth stratum than the low-density pattern and these aggregations are usually composed entirely of hake.

The low- and high-density backscatter patterns also differ with respect to their location in the water column relative to bottom features. For example, the low-density pattern in Figure 4A (in the polygons) is not associated with specific bottom features since it usually occurs 200 m or more below the surface and offshore of the shelf edge, but was observed at depths exceeding 500 m in 2007. Low-density hake aggregations remain discernable within the meso-pelagic acoustic sign attributable primarily to Myctophidae (below the polygons in fig. 4A) in the absence of jumbo squid. In contrast, the high-density pattern is typically observed at or near the shelf break and usually maintains itself within the 200–300 m depth range (fig. 4B). The offshore extent of the high-density hake scattering layer is thought to be associated with high productivity zones linked to ocean upwelling conditions (Mackas et al. 1997; Ressler et al. 2007).

Other species commonly observed during the acoustic survey are also recognizable using signal intensity, morphology, and location criteria. For example, lanternfishes (Myctophidae) largely comprise an indistinct layer of varying intensity, at water depths below 300 m (moderate to dark grey targets in the water below 300 m in fig. 5A). Pacific herring (*Clupea pallasi*) and sardine (*Sardinops sagax*) form dense schools near the surface (<50 m) and produce a characteristic intense (black) "double echo" signal, consisting of an echo in the water column (rec-

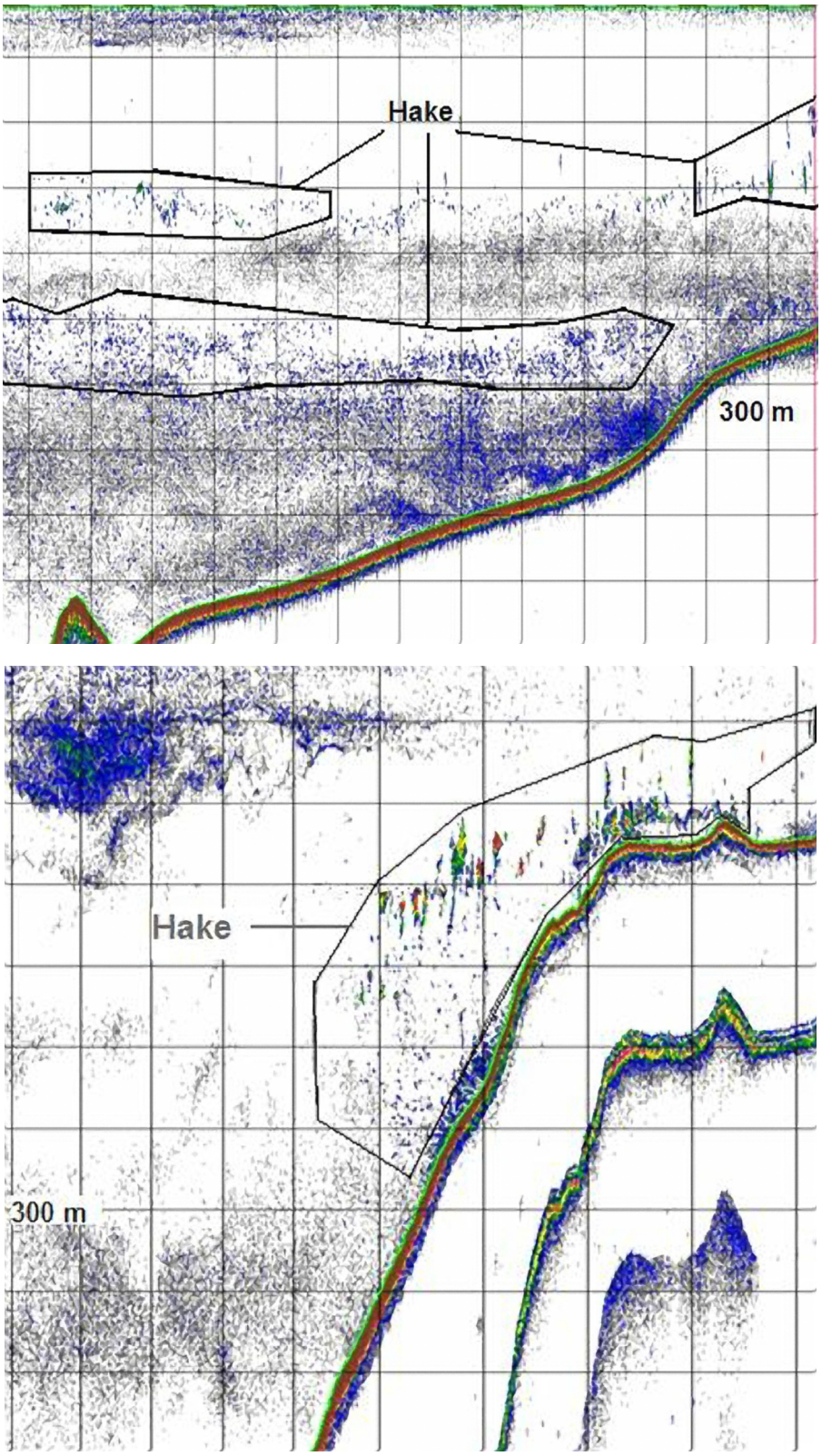

Figure 4. Grey scale examples of low- (A) and high- (B) density hake (*Merluccius productus*) backscatter patterns in 38 kHz echograms observed during the 2007 hake survey. The low-density pattern (in the polygons) was observed on Transect 55 (44.8°N) off Newport, Oregon, at a depth of 260 m on 10 July 2007 at 08:00. The high-density pattern was observed on Transect 29 (40.55°N) off Cape Mendocino, California, at a depth of 120 m on 29 June 2007 at 17:30. Horizontal lines are 50 m depth intervals (300 m is marked) and vertical lines are spaced at 0.5 nmi intervals.

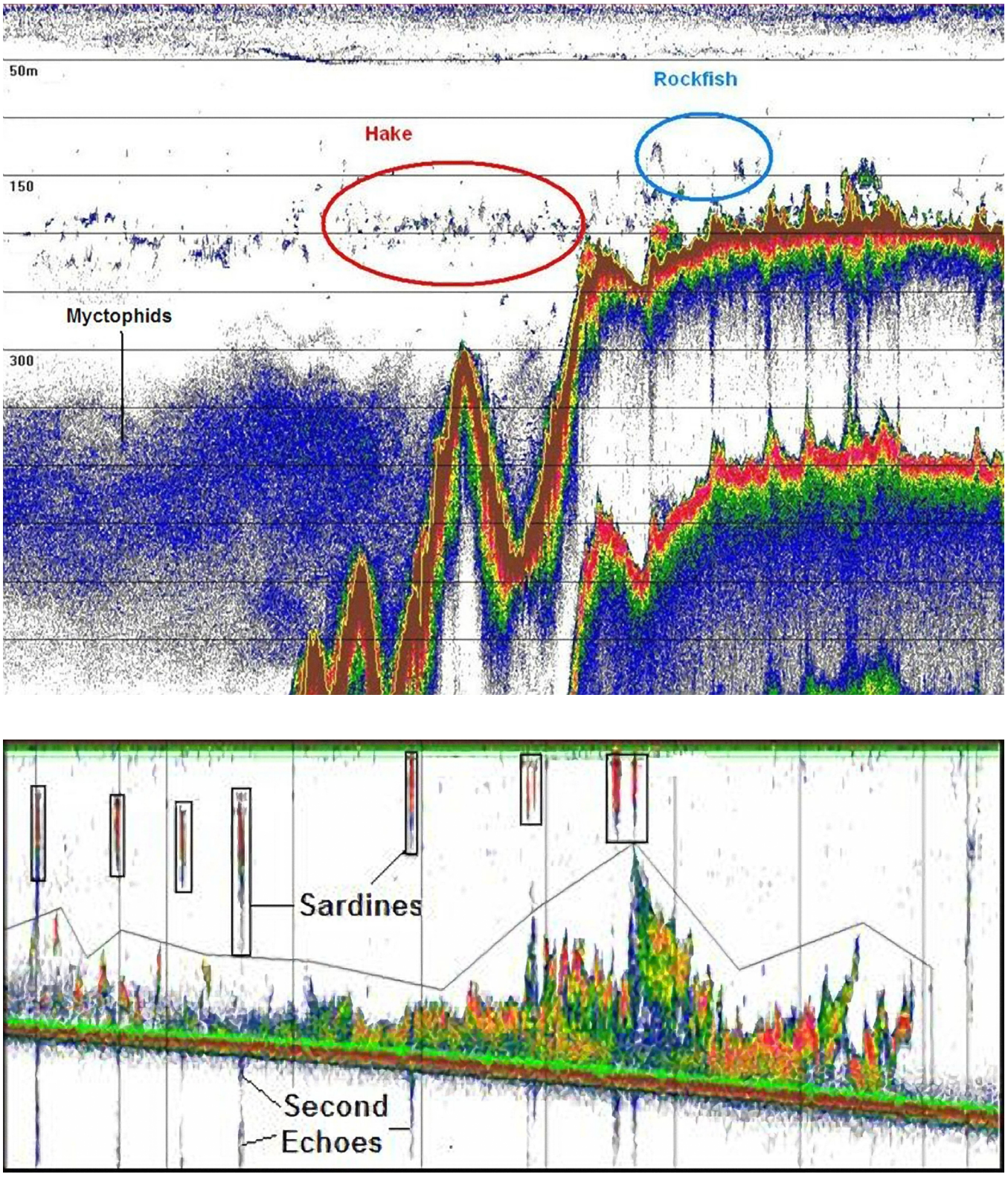

Figure 5. (A) Backscatter patterns near the continental shelf break in 38 kHz echograms from plankton at the surface to 50 m depth, rockfish chimney stacks, hake (*Merluccius productus*), and myctophids below 300 m. The bottom contour trace begins at 600 m depth and rises to 200 m. (B) Double echo returns from dense aggregations of sardine (*Sardinops sagax*) (within polygons) in shallow water over the continental shelf. A second echo aligned in the vertical plane to high-density fish schools can be seen below the bottom contour trace. Vertical lines represent 0.5 nmi intervals along the transect line.

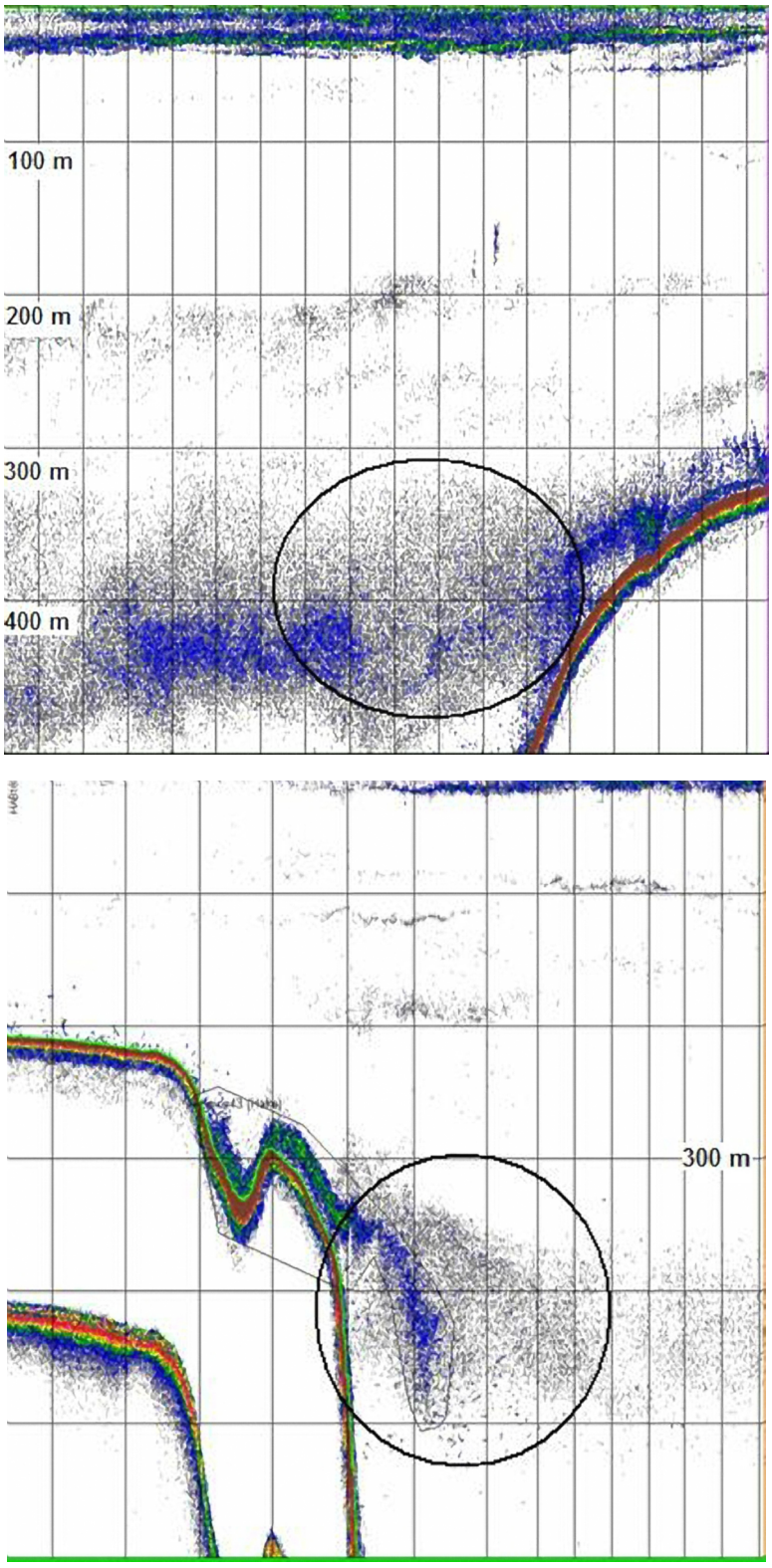

Figure 6. Two examples of mixed hake-jumbo squid backscatter patterns at 38 kHz (circled in A and B) which were considered atypical in 2007 because they resemble low-density layers usually characteristic of meso-pelagic Myctophidae, but contained hake (*Merluccius productus*). (A) Hake and jumbo squid (*Dosidicus gigas*) observed on transects 79 near La Pérouse Bank, British Columbia (48.8°N), at a depth of 350 m on 02 Aug 2007 at 20:25. Trawling on this sign resulted in a catch of 133.5 kg, consisting of 88% jumbo squid and 17% hake. (B) Hake-jumbo squid echogram observed on Transect 89 off northern Vancouver Island (50.5°N), at a depth of 330 m on 07 Aug 2007 at 07:26. A trawl catch of 553 kg consisted of 79% hake and 20% jumbo squid. Horizontal lines are 50 m depth intervals (300 m is marked) and vertical lines are spaced at 0.5 nmi intervals.

tangular polygons in the water column in fig. 5B) and a false echo below the bottom. The sardine aggregations in Figure 5B appear to be moving into or out of a larger aggregation near the bottom. Rockfish (*Sebastes* spp.) typically orient in vertical "chimney stack" formations in association with high-relief bottom types at the shelf edge or further inshore (fig. 5A).

Backscatter patterns at 38 kHz attributable to a mixture of hake and jumbo squid at the locations identified in Figure 3 differed from the hake backscatter patterns observed previously in 2007 and in earlier surveys. A wide diffuse band with few discernable groups and low signal intensity (grey) at depths >300 m was observed at 38 kHz (grey targets in the ellipses in figs. 6A and B). These morphological and signal-intensity features more often characterize myctophid layers (e.g., fig. 5A) rather than a low-density hake layer. In addition, the location of these layers, which were in close association with the shelf break below 300 m and near the bottom, was atypical of hake distribution patterns observed in other surveys. The pattern of hake distribution that we expected, based on experience in previous surveys, is one consisting of a uniform depth distribution across the shelf break, regardless of density. Hake may be near bottom inshore of the edge (fig. 4B) but usually maintain themselves within the zone of high productivity at depths of 200–300 m when seaward of the shelf break (fig. 4A). The unusual patterns observed in 2007 (figs. 6A and B) were only noted in Canadian waters north of 48°N. The normal pattern of hake distribution is related to coastal upwelling conditions, which were not unusual in 2007 relative to the long-term average (fig. 7A), and sea surface temperature, which was near-normal in 2007 (fig. 7B).

DISCUSSION

Jumbo squid is a large, short-lived, pelagic predator. Growth is rapid and allows squid to attain maximum sizes of 1.0–1.2 m dorsal mantle lengths and 30–50 kg during a life span of one to two years (Argüelles et al. 2001; Nigmatullin et al. 2001). Reproduction occurs year round, but peaks in spring and summer, and potential fecundity ranges between 0.3 and 13 million oocytes (Nigmatullin et al. 2001). Migrations for feeding in the summer and fall and spawning in the spring and summer are common (Nigmatullin et al. 2001) and may result in daily movements >30 km (Gilly et al. 2006). Jumbo squid are opportunistic predators of small pelagic and meso-pelagic fishes such as herring and sardines, other cephalopods, and pelagic crustaceans (e.g., Nigmatullin et al. 2001; Markaida and Sosa-Nishizaki 2003; Markaida 2006) and they undertake a diel vertical migration at dusk into near-surface waters to forage (Nigmatullin et al. 2001; Gilly et al. 2006). Tagging studies have demonstrated that squid in the Gulf of California occupy waters below 250 m during daylight hours and that they tolerate and forage in hypoxic conditions in the oxygen minimum layer at these depths because they are able to physiologically reduce oxygen consumption rates under hypoxic conditions (Gilly et al. 2001). Since the probability of catching squid in the upper-mixed layer of the water column during the day is low, future surveys targeting jumbo squid in the northern California Current should implement a sampling strategy that focuses on sampling between dusk and dawn. Short life span, high growth and reproductive rates, and aggressive predation coupled with physiological adaptations that permit tolerance of hypoxic conditions unfavorable to other species are ideal characteristics for invading species and confer competitive advantages to jumbo squid.

Jumbo squid inhabit tropical and subtropical eastern Pacific waters from Chile to the Gulf of California (Nigmatullin et al. 2001) and have spread into the waters off southern and central California (Field et al. 2007) and the Humboldt Current system off Peru (Yamashiro et al. 2007[2]). The earliest anecdotal reports of jumbo squid in eastern Pacific Ocean coastal waters north of central California are two 1997 reports of large numbers off Oregon (Pearcy 2002) and an unconfirmed sighting off Yakutat, Alaska (Cosgrove and Sendall 2004[3]), which were linked by these authors to the strong 1997–98 El Niño event. Cosgrove and Sendall (2004) also reported that jumbo squid were caught well offshore of Vancouver Island during research surveys along the Line P oceanographic line sometime between 1994 and 1998, although this has not been verified or documented by a taxonomic specialist. Following these initial observations, further sightings of jumbo squid were rare until the summer and fall of 2004 and 2005, when incidental catches were made by pelagic fisheries and research surveys off Washington and British Columbia and as far north as Sitka, Alaska (Cosgrove 2005; Trudel et al. 2006; Wing 2006). These jumbo squid occurrences were also considered transient summer range extensions as a result of warm climate-related ocean conditions, rather than El Niño events (Trudel et al. 2006; fig. 7B). The earliest verified catches of jumbo squid during hake acoustic surveys occurred in 2003 off central California. The next survey in 2005 recorded incidental catches in northern California Current waters, and in 2007 incidental catches

[2]Yamashiro, C., R. Castillo, N. Dominguez, C. Paulino, L. Vasquez, and L. Mariategui. 2007. Distribution and abundance of jumbo squid (*Dosidicus gigas*) off the Peruvian coast and their relationships to environmental conditions. Paper S-2 presented at California Cooperative Oceanic Fisheries Investigations Annual Science Conference 2007, Hubbs-SeaWorld Research Institute, San Diego, California, November 26–28, 2007.

[3]Cosgrove, J. A., and K. A. Sendall. 2004. First records of *Dosidicus gigas*, the Humboldt squid, in the temperate north-eastern Pacific. Available at: http://www.royalbcmuseum.bc.ca/Content_Files/Files/Collections%20and%20Research/Natural%20History/Dosidicus_paper.pdf

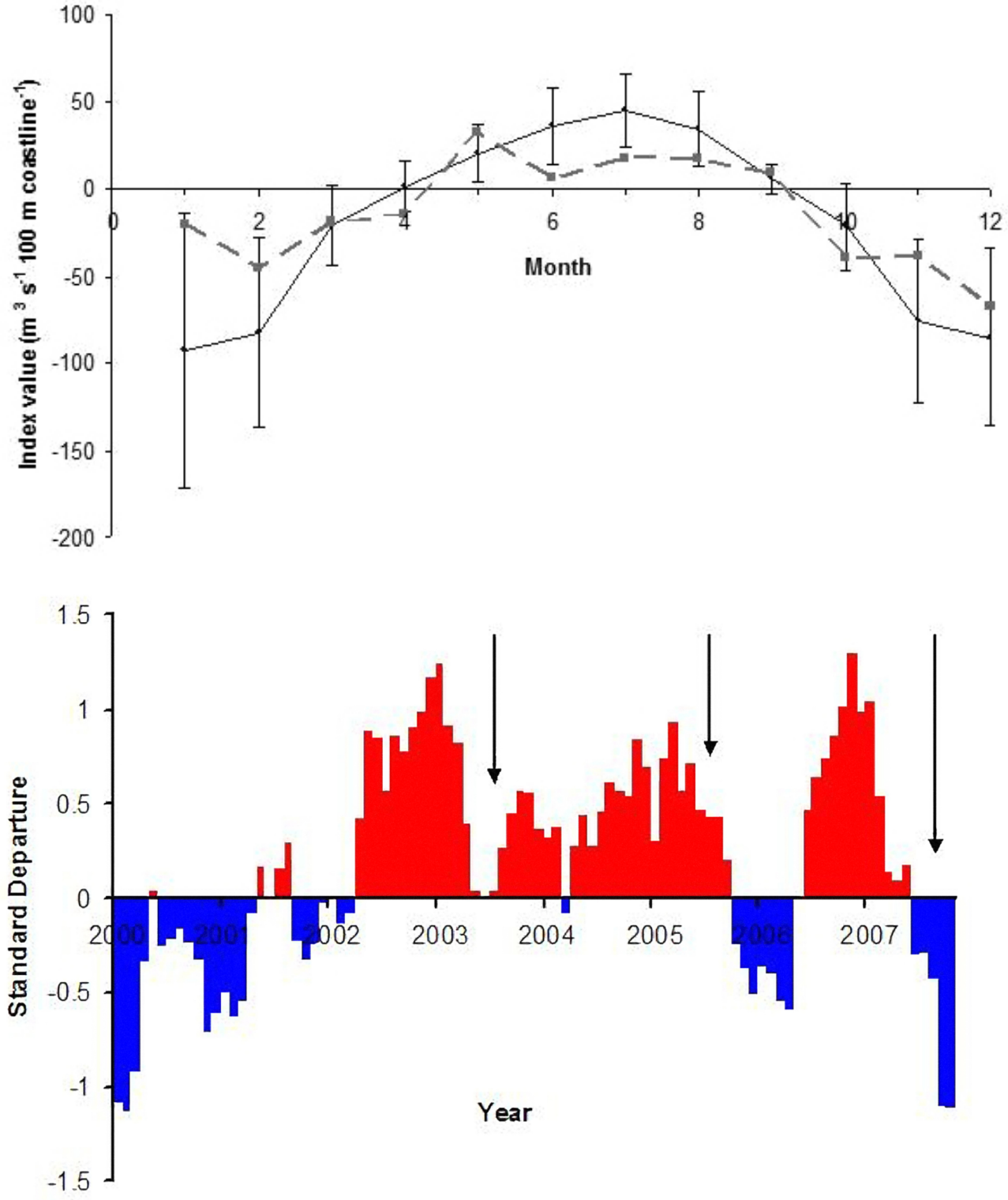

Figure 7. (A) Monthly average upwelling index values ±1 standard deviation for the 1967–91 period at 48°N, 125°W (solid line) and monthly average upwelling values for 2007 (dashed line) at the same location. Positive values denote upwelling and negative values denote downwelling. Data retrieved from http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/data_download.html. See http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/how_computed.html for index computation. (B) Multivariate El Niño-Southern Oscillation index time-series showing periods of warmer (above the *x*-axis) and cooler (below the *x*-axis) ocean conditions, 2000–2007. Arrows mark the approximate timing of hake acoustic surveys in 2003, 2005, and 2007. The MEI is the first unrotated principal component of six variables including sea-level pressure, zonal and meridional components of the surface wind, sea surface temperature, surface air temperature, and total cloudiness fraction of the sky. See Wolter and Timlin (1998) for details. Numerical values of the MEI time-series are available at: http://www.cdc.noaa.gov/people/klaus.wolter/MEI/table.htm.

were made exclusively in these northern waters. The 2007 data do not appear to be a sampling artifact since the distribution of trawl locations and effort between San Francisco and Vancouver Island was not noticeably different from previous surveys.

At present, a self-sustaining population of jumbo squid is likely established off southern and central California as a result of the invasion that occurred in the 2002–06 period (Field et al. 2007; Zeidberg and Robison 2007; Rodhouse 2008). We hypothesize that multiple invasions have occurred in the northern temperate waters of the California Current since 1997 (and perhaps earlier) when climate-related ocean conditions were favorable (warm sea surface temperatures, enhance poleward transport of water), but these occupations did not appear to last very long and have not established a sustained population at present. The evidence supporting this hypothesis consists of anecdotal sightings and incidental catches of squid described above, which show a gap of several years between the earliest reports and more recent sightings. Similar evidence of multiple invasions in Monterey Bay is documented by Zeidberg and Robison (2007).

Our catches of jumbo squid during the 2007 hake survey were notable because the visual appearance of 38 kHz echograms associated with the mixed hake-jumbo squid trawls differed from hake-only trawl echograms. Regional hake distribution is related to sea surface temperature along with coastal upwelling and food production at the shelf break (e.g., Smith et al. 1990; Mackas et al. 1997; Benson et al. 2002), but coastal upwelling conditions in 2007 were not unusual relative to long-term averages (fig. 7A), and sea surface temperatures were near-normal (fig. 7B). Thus, the change in hake behavior is not a regional response to climate-related changes in ocean conditions but may be a response to more localized factors. We hypothesize that jumbo squid predation led to increased swimming activity and dispersal of hake, resulting in the diffuse, less dense aggregation pattern observed near the shelf break in some of the 2007 echograms. We recognize that the evidence supporting this hypothesis is limited to only a few instances in which our trawl catches verified a mixed hake-jumbo squid species composition in 2007 and that this evidence depends on the reliability of the echogram patterns that we described and our association between these patterns and catches. Our echogram interpretations are based on a time series of observations and verifications from trawling operations that provide biological samples of acoustic returns. These interpretations are subjective because judgment is involved, but this subjectivity is reduced through the use of a common group of interpreters for many surveys, the compilation of a catalogue of verified characteristic distribution patterns attributable to various species, including hake, and the development of standardized protocols for scrutinizing and interpreting echograms. Historically, trawling effort at depths >300 m probably has not exceeded 10% in any survey since the low s_A at these depths translates to low hake biomass, which is not a sampling priority given limited vessel availability. However, we have sufficient experience sampling these deep indistinct layers to be confident that they consist primarily of small mesopelagic species such as Myctophidae (see fig. 5A). Despite these caveats, the implications of this hake-jumbo squid interaction hypothesis for Pacific hake acoustic surveys are significant since the acoustic signs associated with mixed hake-squid catches likely would be attributed to small meso-pelagic fishes (e.g., myctophids or lanternfishes in fig. 5A) in the absence of evidence to the contrary. This interpretation would mean that hake in these mixtures will not contribute to overall biomass estimates. If our hypothesis is true and jumbo squid alter the aggregation pattern of hake, then additional ship time and trawling effort may be required in future surveys to identify and verify acoustic signs attributable to hake.

The potential ecosystem impacts of jumbo squid are not known with certainty at present. Zeidberg and Robison (2007) correlated the jumbo squid expansion into Monterey Bay with interactive effects of declines in top predators and climate-related changes in ocean conditions, but did not explicate causal mechanisms leading to declining hake abundance. Field et al. (2007) found that jumbo squid in the California Current preyed heavily on groundfish in the 15–45 cm size range, including hake and several rockfish species (*Sebastes* spp.). These authors also found that larger hake and rockfish were more frequently consumed during winter months off of central California, which is consistent with the migratory pattern of Pacific hake. Jumbo squid caught in winter months tended to be larger (Field et al. 2007) than those caught at other times and were presumably better able to feed on adult fish. Jumbo squid stomachs were not sampled during hake surveys in 2003, 2005, or 2007, so direct evidence of predatory activity on hake is not available. However, the diel vertical foraging migration of jumbo squid at dusk (Gilly et al. 2006) coincides with a vertical migration by hake into near-surface waters after dusk (Ressler et al. 2007), resulting in substantial overlaps in time and space. Further, the ability of jumbo squid to tolerate hypoxic conditions may be advantageous in establishing a multi-generational sustained population in northern waters of the California Current. Whitney et al. (2007) have documented a 17%–30% decrease in oxygen (20–40 μmol/kg) in the depth range 125–300 m at Ocean Station Papa (OSP, 50°N, 145°W) coupled with a shoaling of the hypoxic boundary (defined as 60 μmol O_2/kg) from ~400 to 300 m between 1956 and 2006. These findings are noteworthy because

they imply that hypoxic waters are moving eastward across the Pacific Ocean in the Subarctic Gyre, because coastal upwelling from Oregon to British Columbia draws waters from depths ranging between 100 and >250 m, and because they result in the simple projection that shelf and slope ecosystems will lose oxygenated habitat (Whitney et al. 2007). Species such as jumbo squid that tolerate low oxygen may expand their ranges, but pelagic species such as hake will either shift their distribution or perish. Given the potential overlaps in time and space between hake and jumbo squid, the hypothesis that hake are unlikely to be effective competitors with jumbo squid (Rodhouse 2008), and the knowledge that hake is the most abundant groundfish in the California Current and a key trophic linkage in this system (Ressler et al. 2007), there is ample cause for concern about potential ecosystem impacts. Ecosystem impact modeling that targets trophic interactions associated with jumbo squid invasions is warranted.

We used a simple visual comparison approach to identify mixed hake-jumbo squid acoustic signs. If the presence of jumbo squid continues to increase and disrupt hake behavior, then the application of more sophisticated techniques to identify hake and jumbo squid acoustic signs may be justified. For example, Benoit-Bird et al. (2008) estimated that the average in situ target strength (a measure of acoustic reflectivity) of jumbo squid was about –27.5 dB at 38 kHz, which compares to average in situ values of –33.2 and –35.5 dB reported for hake by Henderson and Horne (2007). These kinds of data could be used as filters in an image analysis procedure designed to automate the isolation and classification of echograms.

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PREDATORY INTERACTIONS AND NICHE OVERLAP BETWEEN MAKO SHARK, *ISURUS OXYRINCHUS*, AND JUMBO SQUID, *DOSIDICUS GIGAS*, IN THE CALIFORNIA CURRENT

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ABSTRACT

Recent scientific and anecdotal observations have documented a range expansion of jumbo squid, *Dosidicus gigas,* into the Southern California Bight (SCB) and northward in the California Current Large Marine Ecosystem. The increase in squid abundance at higher latitudes has generated hypotheses concerning the ecosystem changes that may have permitted this expansion. Top-down explanations suggest that overharvest of higher trophic level species such as tunas and billfishes creates a trophic cascade that increases survivorship of jumbo squid. Bottom-up explanations suggest that changes in ocean climate, including temperature and hypoxia, may favor an expanded range for jumbo squid. Here we present information on: (1) predatory interactions between the mako shark and jumbo squid in the SCB, (2) vertical niche of mako sharks and potential for a hypoxic refuge for jumbo squid, and (3) changes in the oxygen minimum zone (OMZ) and trends in epi- and mesopelagic prey. Mako sharks examined during the 2006 and 2007 NOAA Fisheries Southwest Fisheries Science Center Juvenile Shark Longline Survey had a high incidence of scars inflicted by jumbo squid. Diet studies based on the California Drift Gillnet Fishery, 2002–07 indicate that jumbo squid accounted for a substantial portion of the mako diet. Bioenergetic calculations suggest that the average 18 kg mako taken in the fishery would need 56–113 kg of squid to meet its annual dietary requirements. The high-resolution diel activity records of two representative animals indicate makos remained near the surface at night and were able to exploit the water column from the surface to a maximum depth of 300 m during the day. The maximum depth of dives corresponded to oxygen concentrations as low as 1.25 ml/L. Previous studies indicate that jumbo squid inhabit a depth range from the surface to the upper bounds of the OMZ where oxygen concentration is 0.5 ml/L or less. Jumbo squid in the SCB may have a deepwater refuge from mako sharks below 1.25 ml O_2/L, but are clearly available to mako during diel vertical migrations. Examination of the CalCOFI database for changes in oxygen content and larval fish counts over the previous 56 years indicates a shoaling of the OMZ and periodic changes in abundance of epi- and mesopelagic prey species, but did not reveal a simple relationship between oxygen, prey availability, and range expansion. Better estimates of squid and mako population size and mako removal rates are needed to fully understand the impact of mako sharks on jumbo squid abundance.

INTRODUCTION

The jumbo squid, *Dosidicus gigas*, is a dominant mid-trophic link in the pelagic food webs of the Eastern Tropical Pacific (ETP; Olson and Young 2007). Recent studies originating in the Gulf of California (GOC), where jumbo squid are permanent residents, have described their age and growth, reproductive biology, and trophic niche (Markaida and Sosa-Nishizaki 2001, 2003; Markaida et al. 2004). Electronic tagging studies have provided new insights into the physical niche including horizontal and vertical movements, diel activity patterns, preferred temperatures, and a previously unappreciated tolerance of low-oxygen, mesopelagic habitats (Gilly et al. 2006). The mesopelagic oxygen minimum zone (OMZ) is a persistent feature of the ETP (Stramma et al. 2008) and extends northward throughout the California Current Large Marine Ecosystem (CCLME) usually at depths of 600 to 1000 m (Vetter and Lynn 1997; Chan et al. 2008). Two recent studies (Field et al. 2007; Zeidberg and Robison 2007) have reported a range extension of jumbo squid into the colder waters of the central California Current where they have been observed to a depth of 2000 m. Historically, the occurrence of the jumbo squid off California was restricted to periodic outbreaks, often associated with El Niño-Southern Oscillation (ENSO) events (Rodhouse, this volume). Interest by scientists, management agencies, and the general public has driven speculation on how the CCLME may be changing to allow this persistent northern range expansion. Proposed causes can be grouped into two categories: (1) top-down effects, such as removal of squid predators and competitors by fishing, which might increase jumbo squid survival and (2) bottom-up effects, such as changes in oceanography and prey fish abundance, that might increase favorable jumbo squid habitat. These speculations are not without controversy

(Watters et al. 2008; Zeidberg and Robison 2008) and are based on limited data. The Southern California Bight (SCB) has not been a focus of jumbo squid research but has been a focus of many long-term observing programs (e.g., California Cooperative Fisheries Investigations or CalCOFI). Records of potential jumbo squid predators (both fish and marine mammals), prey species, and baseline measurements of physical variables, such as oxygen saturation, are reasonably well known and may provide insights into the importance of top-down and bottom-up effects on jumbo squid abundance and persistence.

One apex predator that could affect jumbo squid in the SCB is the shortfin mako shark, *Isurus oxyrinchus* (Rafinesque 1810). The shortfin mako shark, herein referred to as mako shark, is a lamnid shark that inhabits temperate and subtropical seas worldwide (Compagno et al. 2005). Off the U.S. West Coast, the mako is a relatively abundant apex predator that utilizes the rich resources of the CCLME. In the U.S. West Coast Exclusive Economic Zone (EEZ) it is subject to both commercial and recreational fisheries (Cailliet and Bedford 1983; Hanan et al. 1993; Holts et al. 1998) and is managed under the Pacific Fishery Management Council's Highly Migratory Species Fisheries Management Plan as well as under state regulations (PFMC 2003). The SCB, between Point Conception and Cape Colonet, Baja California, Mexico, is said to be an important pupping and nursery area (O'Brien and Sunada 1994). As such, the majority of the U.S. West Coast commercial catch consists of neonates and juveniles of less than 145 cm fork length (FL) and estimated ages 0 to 3 (Hanan et al. 1993; O'Brien and Sunada 1994; PFMC 2003). Reproductively mature individuals are uncommon but seasonally targeted by the recreational fishery.

As is typical of members of the family Lamnidae, the mako shark is endothermic and has important physiological and biochemical adaptations that increase oxygen delivery, maintain high aerobic muscle performance and allow heat retention (Bernal et al. 2001). These adaptations are reflected in the mako's high metabolic rates (Graham et al. 1990; Sepulveda et al. 2007) resulting in a high caloric demand and daily ration (Stillwell and Kohler 1982). High aerobic activity may also limit foraging under low oxygen conditions. Although comprehensive diet studies of makos off the U.S. West Coast have not yet been conducted, the available data indicate that sub-adults here and elsewhere consume a diet primarily composed of fish and cephalopods with larger sharks consuming billfishes and marine mammals on occasion (Mearns et al. 1981; Stillwell and Kohler 1982; PFMC 2003).

To provide biological information for the management of mako sharks, the NOAA Fisheries Southwest Fisheries Science Center (SWFSC) is actively engaged in the study of their migratory patterns, foraging activities, life-history characteristics, and population demographics. Primary sources of data include: (1) a long-standing research cruise, the Juvenile Shark Longline Survey (JSLS) conducted by the SWFSC, (2) fishery observers monitoring the California Drift Gillnet Fishery (CDGNF), and (3) the SWFSC CalCOFI survey that monitors ocean productivity and forage fishes. Through the JSLS, information on population biology and abundance is obtained and the survey provides a platform for biological sampling and traditional and electronic tagging studies. The CDGNF targets swordfish (*Xiphias gladius*), but mako sharks are an important and valuable incidental catch. Fishery observers aboard 20% of the trips monitor all catch and conduct biological sampling of stomachs, DNA, and gonads in support of studies on age, growth, reproduction, and diet. Both the survey and fishery focus on the SCB from Point Conception to the U.S.-Mexico border. The CalCOFI sampling program, in addition to shipboard measurements taken in conjunction with the JSLS and the CDGNF observer program, provides a time series of oceanographic data to help characterize the mako shark's habitat in the SCB.

In this paper we present recent observations on the mako shark-jumbo squid association and climate variables as they relate to the apparent increase and persistence of jumbo squid in the SCB. We discuss horizontal and vertical movements of mako sharks in the SCB as revealed by electronic tagging, the relationships between maximum dive depths and the thermal and oxygen profile of the mako shark and jumbo squid habitat, the extent of mako shark predation on jumbo squid, and the potential bioenergetic consequences of mako shark predation at the population and ecosystem levels. We also discuss changes in the oxygen structure of the SCB and changes in abundance of epi- and mesopelagic fishes as revealed by the CalCOFI oceanographic and ichthyoplankton time series. Our intent is to summarize recent observations within the SCB portion of the CCLME as they pertain to predatory interactions and niche overlap of mako shark and jumbo squid.

MATERIALS AND METHODS

JSLS Procedures and Visual Observations of Squid Scars

The JSLS has been conducted most summers since 1994 in the SCB aboard the NOAA RV *David Starr Jordan*. Sharks are caught during daylight hours using shallow-set longline gear baited with Pacific mackerel (*Scomber japonicus*). Two four-hour sets are conducted daily, each with two miles of stainless steel gear and 200 hooks set in the top 30 m of the water column. If a shark is caught, it is led to the stern of the vessel and restrained

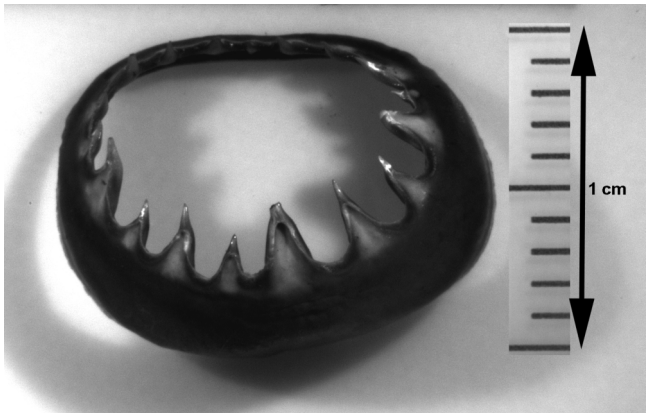

Figure 1. Toothed ring from the sucker of a feeding tentacle of *Dosidicus gigas* collected in the Southern California Bight during NOAA Fisheries Juvenile Shark Longline Survey.

in a specially designed cradle at the waterline. Depending on research needs (see below) different measurements and procedures may be performed, but at a minimum the hook is removed, total length or FL, sex, and species are recorded, the animal is tagged with conventional tags, and a DNA sample (fin clip) is obtained. Prior to release, each animal is evaluated for overall condition and assigned a score of poor, fair, good or excellent. During the condition evaluation there is time to observe scarring due to previous encounters with fishing gear, mating bites, or encounters with jumbo squid. Each sucker on the squid's arms and tentacles contains a ring of small grasping teeth (fig. 1) that produce characteristic marks (Barnes 1987; Nesis 1987).

Electronic Tagging

To study the migratory patterns of mako sharks in the CCLME, we have been deploying electronic tags during the JSLS as part of a SWFSC and Tagging of Pacific Pelagics (TOPP) collaborative project. Tags deployed include pop-off archival tags (PAT) which record water temperature, depth, and light level at one-minute intervals, and radio transmitting satellite-linked position tags (SPOT) which can be tracked through the Argos system (www.clsamerica.com) to provide horizontal movement information. The PAT (Wildlife Computers, Inc.) is anchored in the dorsal musculature near the first dorsal fin and the SPOT (Wildlife Computers, Inc.) is mounted high on the first dorsal fin so that it transmits whenever the fin breaks the surface of the water.

For this study, we focused on the behavior of two mako sharks that remained in the SCB during the fall months. For both sharks, we have detailed archival data due to the recovery of the PAT and accurate location estimates from the SPOT tags. The first shark, Mako1, was a 114 cm total length (TL) male tagged on 29 July 2004 with a model PAT3 tag and a model SPOT4 tag. The second shark, Mako2, was a 191 cm TL male tagged on 30 June 2006 with a model PAT5 tag and a model SPOT5 tag. To examine their behaviors with respect to specific habitats within the SCB (i.e., nearshore vs. offshore), we identified archival data for which reliable Argos positions (location classes 1-3) indicated overlap in time and space with the CDGNF and the stomach sampling program.

Diet Analyses

Stomachs of mako sharks were collected during the 2002–06 fishing seasons by NOAA Fisheries observers aboard CDGNF vessels targeting swordfish. Sampling months were August through January and the majority (93%) of stomachs was collected within the SCB where the fishery is currently concentrated. The date, time and location of capture, shark FL and sex were recorded. Stomachs were frozen onboard and later transferred to the SWFSC La Jolla, California, laboratory where they were processed within six months.

Stomach contents were analyzed to the lowest possible taxon following the methods of Preti et al. (2001) using keys when necessary to identify species from hard parts (e.g., Clothier 1950; Iverson and Pinkas 1971). Data were analyzed for each season by prey taxa for relative measures of prey quantities (RMPQs) as follows: percent occurrence by number (%N), percent frequency of occurrence (%FO), and percent occurrence by weight (%W) of prey items. The value %N is the number of individuals of a specific taxon found in all stomachs divided by the total number of all prey found times 100; %FO is the number of stomachs containing prey of a specific taxon divided by the total number of stomachs containing prey times 100; %W is the total weight of all remains of a specific taxon divided by the total weight of all prey remains found times 100 (Hyslop 1980; Preti et al. 2001). Weight was the actual weight of the prey remains, not the estimated weight of prey at ingestion. Empty stomachs, slurry, and detritus were not used when calculating percentages. The values listed above were used to calculate the Geometric Index of Importance (GII). The GII, in its simplified form, is calculated as:

$$GII_j = \frac{\left(\sum_{i=1}^{n} V_i \right)_j}{\sqrt{n}}, \quad (1)$$

where GII_j = index value for the j-th prey category, V_i = the magnitude of the vector for the i-th RMPQ of the j-th prey category, and n = the number of RMPQs used in the analysis. In our study this is expressed as:

$$GII_j = (\%N_j + \%W_j + \%FO_j)/\sqrt{3}. \quad (2)$$

TABLE 1
Bioenergetic calculations used to convert metabolic estimates for an average 7 kg mako shark, *Isurus oxyrinchus*, to the amount of jumbo squid, *Dosidicus gigas*, consumed by mako sharks caught in the California Drift Gillnet Fishery.

Action	Process	Result	Reference
Energetic Cost			
Active metabolic rate	Mid-point between routine and max metabolic rate	443 mg O_2/kg/h for mean 7 kg shark	Sepulveda et al. 2007
Scale to 18 kg shark	Scaling exponent = 0.75	349 mg O_2/kg/h	Schmidt-Nielson 1997, Williams 1999
Convert mg O_2 to J	1 mg O_2 = 13.6 J	4752 J/kg/h	Jobling 1994
Add % lost to waste	Waste = 27%	6035J/kg/h	Brett and Groves 1979
Convert J to kg squid	1 kg squid = $4.22*10^{-6}$ J	$1.43*10^{-3}$kg squid/kg/h	Cauffope and Heymans 2005
Convert to kg squid per shark per year	Modal shark = 18 kg	226 kg squid/y	NMFS observer data
Assume 25–50% of diet is squid		56–113 kg squid/shark/y	
Sharks Caught Annually			
Average Annual Landings 1981–2006		163,000 kg	PFMC 2007
Estimate number of sharks	Modal shark = 18 kg	9056 sharks	NMFS observer data
Squid Consumed			
Squid consumed by sharks caught	Assume 25-50% of diet	511–1021 mt squid/y	

We examined the sizes of squid consumed by sharks of different sizes. To calculate the mantle length (ML) of jumbo squid, upper rostral length (URL) was measured and the regression equation from Markaida and Sosa-Nishizaki (2003) was used:

$$ML = 129 + 30.5\ URL, \quad (3)$$

where the unit for ML and URL is mm.

Stomach contents were also examined during the JSLS from sharks which were collected for other ongoing biological studies. Because of the difference in sampling protocols, these stomachs were not included in the analysis to characterize mako diets. However, *D. gigas* remains were found in five stomachs of mako sharks of measured size (two samples from June 2004 and three from July 2007) and those beaks were measured and included in the relationship between prey size (squid mantle length as estimated from URL) and mako size.

Bioenergetic Estimates of Mako Metabolism and Ration

To calculate the energy requirements of the mako shark, standard energetic equations and equivalents were used (tab. 1). First, the active metabolic rate was estimated by taking the midpoint between the routine and maximum rates of oxygen consumption determined by Sepulveda et al. (2007). This resulted in a 29% increase above routine values. Similarly, in their study, Stillwell and Kohler (1982) added 25%–50% to adjust the routine metabolic estimate of mako sharks to an active metabolic estimate. Metabolic rate was estimated for a shark of modal weight taken in the CDGNF during the period 1990–2006 (NMFS observer data; SWFSC) using a scaling exponent of 0.75 (Schmidt-Nielsen 1997; Williams 1999). To convert mg O_2 to Joules (J), the oxycalorific equivalent, 13.6 J = 1 mg O_2 (Jobling 1994), was used. This value was then adjusted for waste, assuming that 27% of ingested energy is lost (Brett and Groves 1979). To determine the mass of squid needed to provide the required energy to an average mako shark, J values were converted to mg of jumbo squid using 4.22 J = 1 mg (Cauffope and Heymans 2005). Finally, the overall energetic requirements of the population of mako sharks typically harvested in the CDGNF were calculated based on the annual fishery landings.

Methods of Analysis of Physical Oceanographic Data from CalCOFI

We used the Scripps Institution of Oceanography CalCOFI hydrographic database to compare the depth of the oxygen minimum layer between two five-year time periods (1951 to 1955 and 2001 to 2005). The survey domain was more extensive in the earlier period, so the comparison was only made for the SCB. We operationally defined the depth of the oxygen minimum layer as the depth of the 0.5 ml O_2/L isopleth (Mullins et al. 1985; Vetter et al. 1994). We averaged isopleth depths over July to December for all five years, and plotted the mean oxygen minimum layer depths as two isosurfaces for visual comparison.

Methods of Analysis of Ichthyoplankton Data from CalCOFI

Larval fish abundance can be used as an indicator of adult spawning biomass for many fish species (Lasker 1985; Ralston et al. 2003; Lo 2007). We obtained a CalCOFI time series (between 1951 and 2006) of larval fish data to examine trends in abundance of six species that are common prey in the diets of jumbo squid and mako sharks in the CCLME (Field et al. 2007; Preti

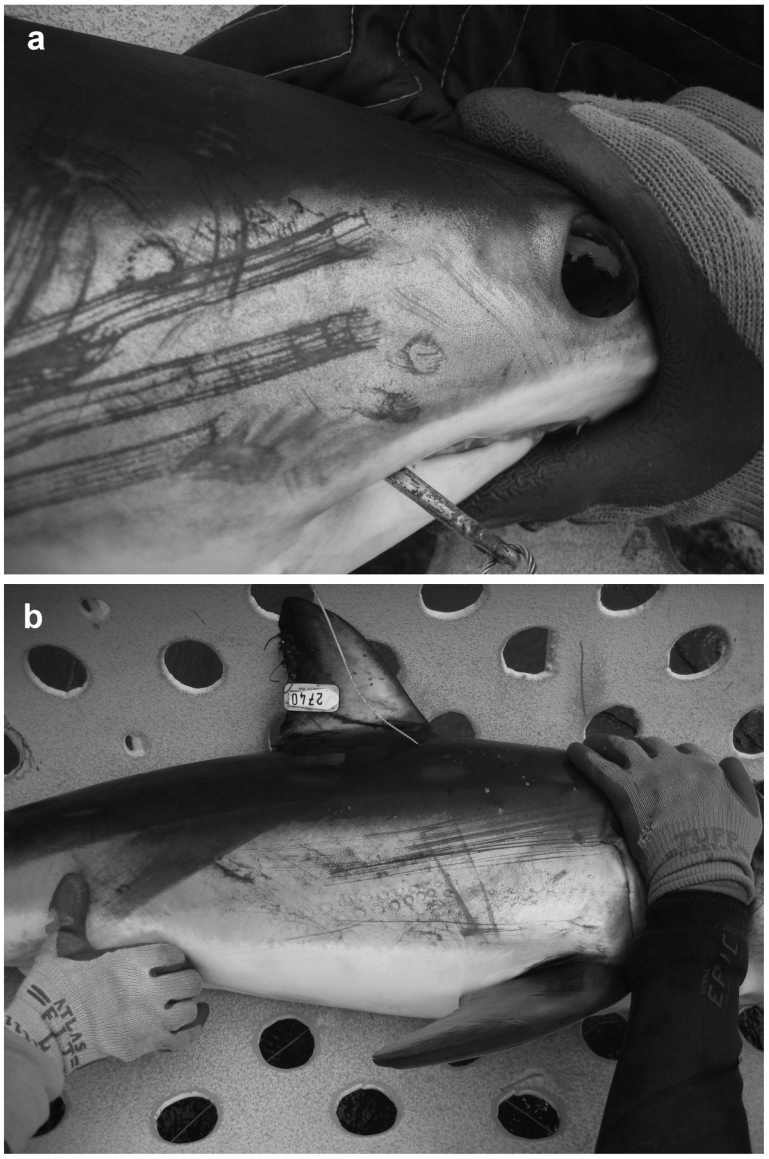

Figure 2. Shortfin mako sharks, *Isurus oxyrinchus*, in tagging cradle of RV *David Starr Jordan* during 2007 JSLS. (a) Scarring due to jumbo squid, *Dosidicus gigas*, sucker marks appear as rings of small incisions and as track marks that begin as a circular ring and continue as scratches across the skin of the animal. Marks are most prominent around the mouth of the mako. (b) Circular scarring and tracks on the midsection of a small mako.

et al., unpubl. data). They include northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), hake (*Merluccius productus*), shortbelly rockfish (*Sebastes jordani*), and two mesopelagic myctophid fishes, blue lanternfish (*Tarletonbeania crenularis*) and northern lampfish (*Stenobrachius leucopsarus*). Standardized larval abundances (number of larvae in $10/m^2$) were spatially averaged for each survey over all standard CalCOFI stations in the SCB for cruises during the spawning periods of each species (Moser et al. 2001). Larval abundances were scaled by subtracting the series mean and centered by dividing by the root mean square to make the time series comparable before plotting.

RESULTS

Visual Observations of Squid Scars on Mako Sharks

Observations made during the JSLS revealed that mako sharks are frequently covered with scars from jumbo squid. The scars appeared as a ring of small incisions (fig. 2a), or a series of parallel, linear scars, suggestive of the sucker and its teeth having been dragged along the skin (fig. 2b). Linear scars often begin with a circular mark on the shark's midsection and lead forward towards the mouth of the shark. The nature of the scars suggests that they were made as the shark ingested the jumbo

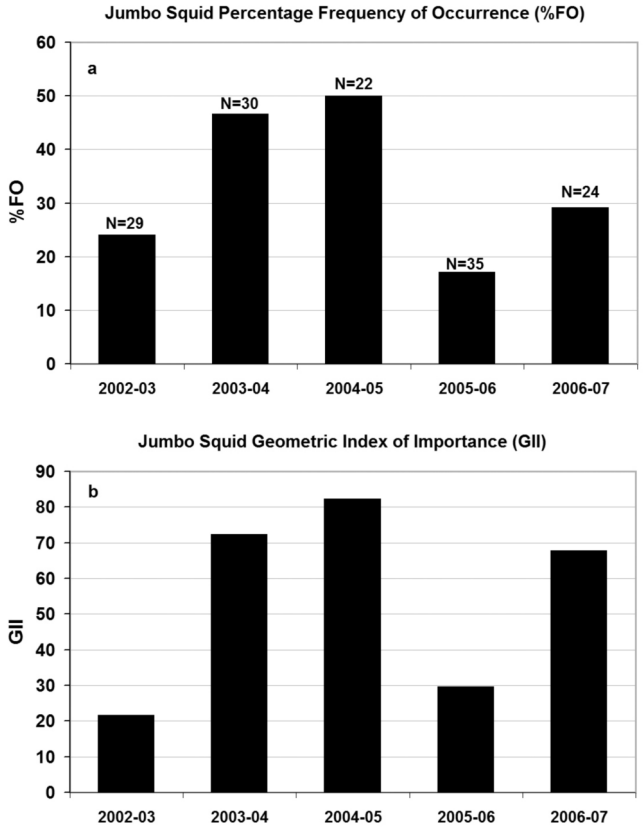

Figure 3. (a) Jumbo squid, *Dosidicus gigas*, percentage Frequency of Occurrence (%FO) in mako shark, *Isurus oxyrinchus*, stomachs by season (*N* = 140 stomachs with food). (b) Results of Geometric Index of Importance (GII) analyses for jumbo squid by season (*N* = 140 stomachs with food).

squid. Squid sucker marks have been observed on blue (*Prionace glauca*) and common thresher sharks (*Alopias vulpinus*), but the marks are faint and infrequent compared to those on makos. Although similar scars have occasionally been observed on makos during cruises prior to 2005, there is a general impression among the authors (Vetter and Kohin) that the frequency of occurrence and amount of scarring have increased and were particularly noticeable in 2006 and 2007.

Mako Shark Diet Studies

Analysis of 140 mako stomachs containing prey collected over five fishing seasons (2002–03 to 2006–07) reveals a high frequency of occurrence for jumbo squid in the stomachs of sharks captured in the CDGNF (fig. 3a). Shark FL ranged from 52 to 248 cm. Percent frequency of occurrence varied from 50% in 2004 to 17.1% in 2005. The mean %FO was 32.1%, indicating that over the five fishing seasons almost a third of the stomachs with prey contained jumbo squid.

The geometric index of importance, GII, which is a function not only of %FO, but also %N and %W, tends to vary more than the %FO alone. Nevertheless, the GII clearly shows the importance of jumbo squid in the diet of makos caught in the CDGNF (fig. 3b). The GII can theoretically take on a maximum value of 173 in this analysis if there is only one prey taxon found in all stomachs. The GII for jumbo squid was always over 20 and had a maximum value of over 80 in 2004–05, indicating a high relative importance in the mako diet.

The stomach contents of animals that died during the JSLS were compared to those collected through the CDGNF observer program. Six mako stomachs examined from the 2004 and 2007 JSLS contained remains of jumbo squid, confirming their presence in the SCB during the summer months.

The derived mantle length of jumbo squid ingested by makos of different sizes is shown in Figure 4. While there is a positive correlation between the size of squid consumed and shark length ($r = 0.413$, $df = 66$, $p < 0.001$), even the smaller sharks consumed relatively large squid. The smallest mako sharks likely represent age 0–1 sharks and are not much larger than the published birth weights (60–70 cm TL; Compagno et al. 2005).

Mako Shark Horizontal Movements

We examined in detail the horizontal movements of two mako sharks tagged with electronic tags. Both sharks were tagged during the summer and spent up to five months in the SCB (fig. 5). Shark movements appeared directed at times when the animals transited rapidly, while at other times daily movements were much slower and the sharks remained in relatively focused areas for a week at a time or longer. When movements were restricted to focal areas offshore, horizontal movements averaged 13.9 km/day for Mako1 and 17.0 km/day for Mako2. When movements were restricted to a very small area in Santa Monica Bay, horizontal movements averaged 4.4 km/day for Mako1 and 2.0 km/day for Mako2. In contrast, during periods when the sharks demonstrated directed movements transiting between focal areas, rates of movements averaged 49.2 km/day for Mako1 and 45.6 km/day for Mako2. Based on their horizontal behaviors, we concluded that the sharks were likely foraging when in the focal areas offshore and within Santa Monica Bay (Le Boeuf et al. 2000; Tremblay et al. 2007). Thus, we examined the diving behavior and oceanographic conditions within these foraging areas to make inferences about the potential for mako and jumbo squid interactions.

Mako Shark Vertical Movements

In the offshore areas, both mako sharks spent greater than 99% of their time in the top 75 m of the water column (fig. 6a and c). Surface-water temperatures were lower in the offshore areas than near shore; however, even with occasional dives through the thermocline, 98%

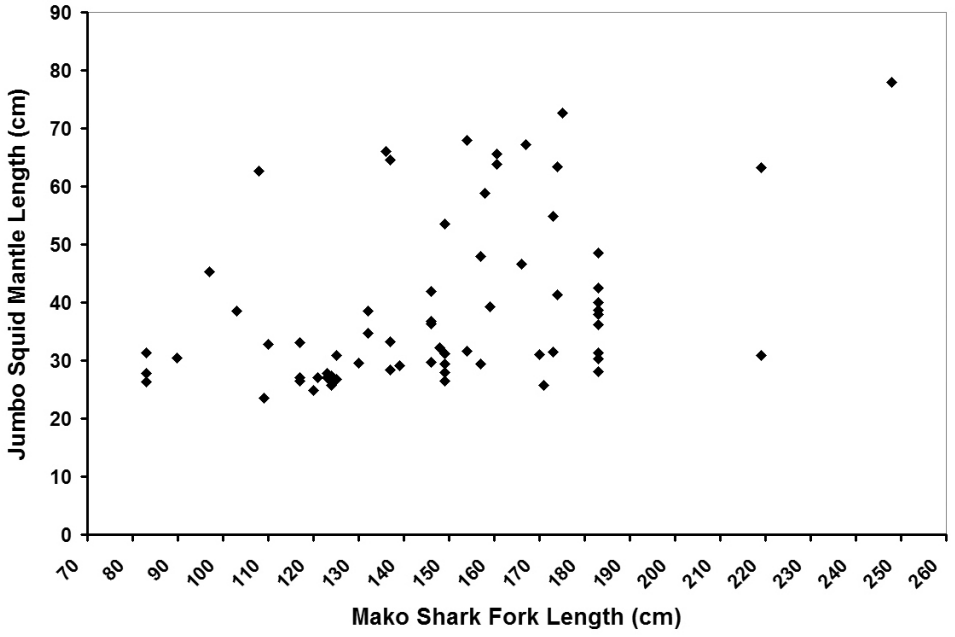

Figure 4. The relationship between mako shark, *Isurus oxyrinchus*, size (fork length in cm) and jumbo squid, *Dosidicus gigas*, size (estimated mantle length in cm) found in the stomachs of mako sharks.

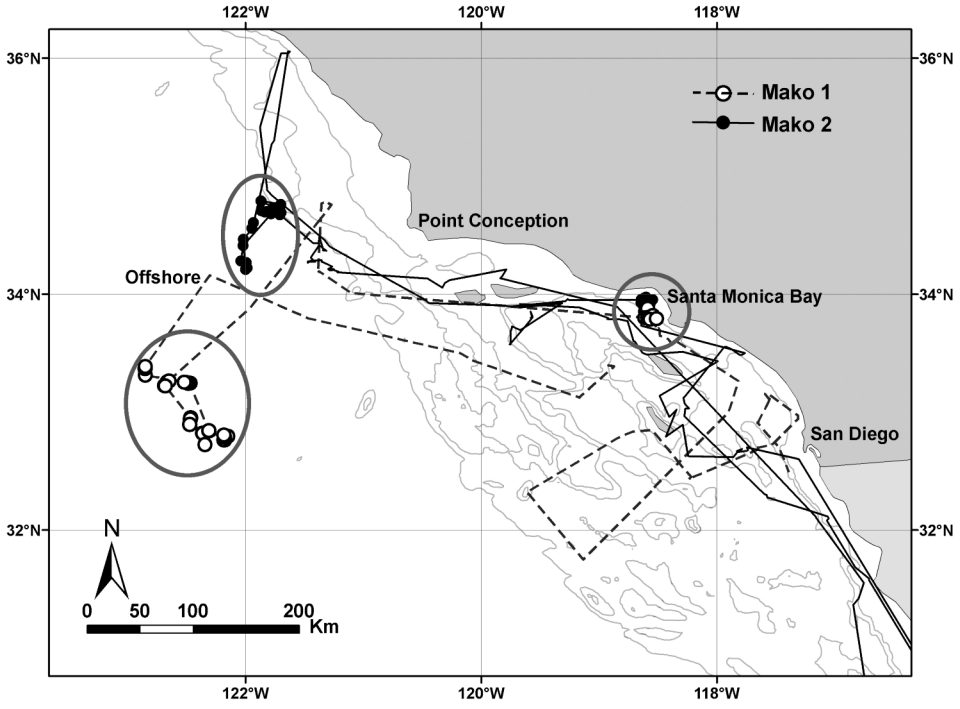

Figure 5. Horizontal movements of two mako sharks, *Isurus oxyrinchus*, in the SCB. Focal foraging areas where vertical behavior was examined include Santa Monica Bay and two areas offshore. Isobaths are 500, 1000, and 2000 m.

of their time was spent in waters warmer than 12°C. In contrast, in Santa Monica Bay, both sharks spent proportionately more time at depths exceeding 100 m (Mako1: 23.9%; Mako2: 18.5%; fig. 6b and d). Because of the greater diving activity, more time was also spent in water colder than 12°C (24.3% and 13.2%, respectively). The greatest depth and coldest temperatures experienced by either shark in the focal areas was 324 m and 8.9°C. During excursions to depth in the Santa Monica Bay area, Mako1 experienced low dissolved oxygen levels. CalCOFI data for that time and area indicate that the 1.5 ml O_2/L isopleth is at approximately 245 m,

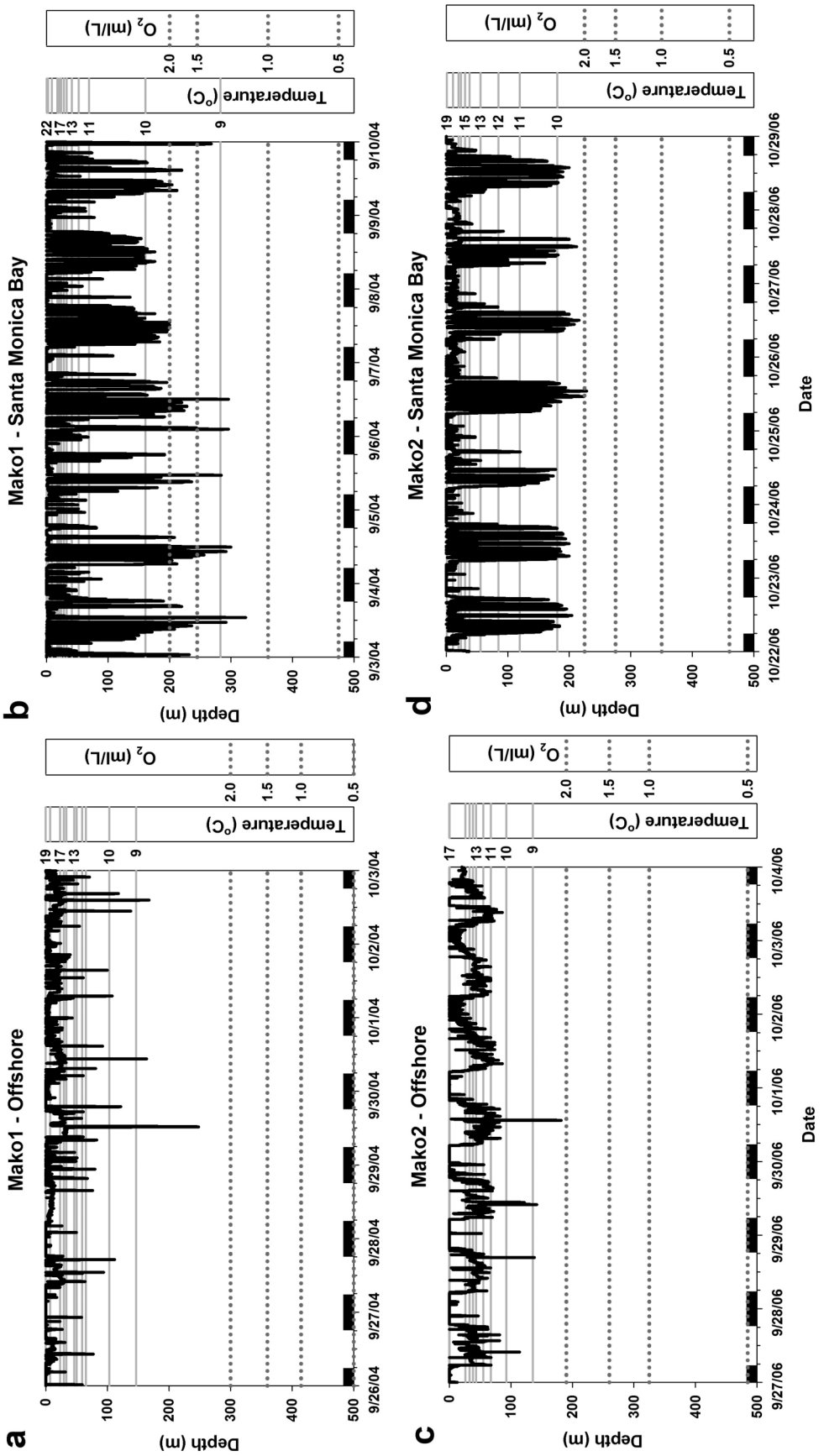

Figure 6. Vertical behavior of the two mako sharks, *Isurus oxyrinchus*, in the focal foraging areas. Black bars along the *x* axis indicate night periods.

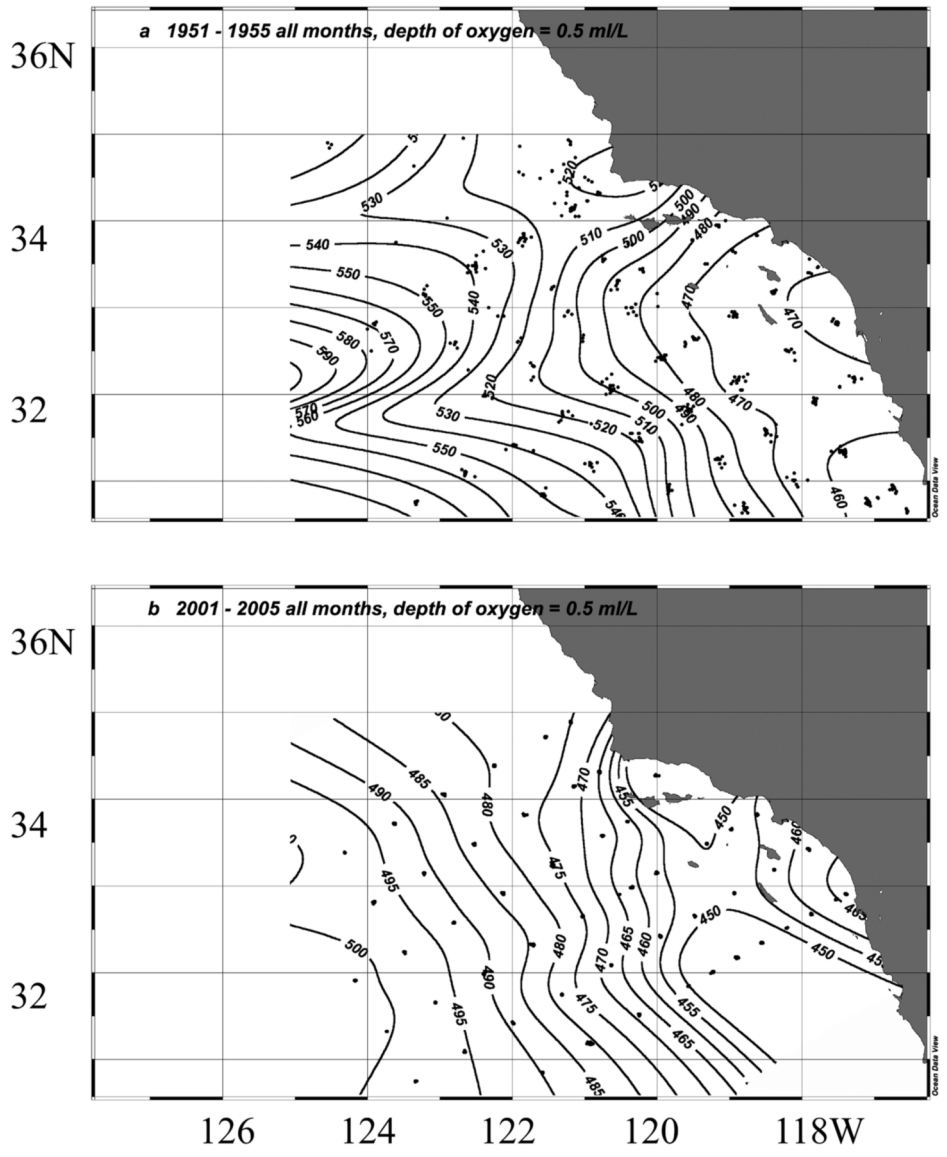

Figure 7. Comparison of the depth of the oxygen minimum layer (defined as 0.5 ml O_2/L concentration) between (a) 1951–55 and (b) 2001–05 in the Southern California Bight. Stations sampled in all of these years are shown as black dots.

TABLE 2

Comparison of ranked frequency of occurrence in the diet of jumbo squid, *Dosidicus gigas*, in the CCLME (Table 2 in Field et al. 2007) compared to the ranked abundance of fish larvae as they occur in the CalCOFI ichthyoplankton data (1951–98). Rankings are based on the 301 most common larval fish taxa identified to the lowest taxonomic unit (Table 4 in CalCOFI Atlas 34, Moser et al. 2001).

Common Name	Scientific name	Rank in Jumbo Squid Diet	Rank of Fish Prey Only	CalCOFI Larval Abundance Rank
Pacific hake	*Merluccius productus*	1	1	2
northern lampfish	*Stenobrachius leucopsarus*	2	2	6
northern anchovy	*Engraulis mordax*	3	3	1
blue lanternfish	*Tarletonbeania crenularis*	4	4	18
Pacific sardine	*Sardinops sagax*	5	5	7
shortbelly rockfish	*Sebastes jordani*	7	6	9
California headlightfish	*Diaphus theta*	8	7	29
broadfin lampfish	*Nannobrachium ritteri*	10	8	17
rockfish spp.	*Sebastes* spp.	11	9	4
California lanternfish	*Symbolophorous californiensis*	14	10	23

below which the shark dove on nine occasions. The longest excursion to depths greater than 245 m and with O_2 at levels less than 1.5 ml O_2/L was 19 minutes. Overall, the two mako sharks rarely encountered O_2 levels below 2 ml/L. For both sharks, there was a diel pattern of activity which was particularly pronounced in the Santa Monica Bay area; more time was spent making vertical excursions through the water column during the day, while the sharks generally remained within the upper mixed layer at night.

Bioenergetics and Trophic Considerations

Based on the modal size of makos taken in the CDGNF and the average total landings, the estimate of jumbo squid consumed by the makos harvested in the fishery is 511–1021 mt annually (tab. 1). The estimated size of the total population of makos in the CCLME is presently unknown.

Changes in the Depth of the Oxygen Minimum Zone

Visual comparison of the isosurfaces for the 0.5 ml O_2/L oxygen minimum layer over time reveals that the depth of the OMZ is shallower inshore compared with offshore and has shoaled in both regions over the last 50 years (fig. 7). The OMZ was about 30 to 70 m shallower offshore in 2001–05 compared to 1951–55. The depth of the OMZ inshore shoaled by about 20 m over the same period, which was a less marked change than offshore. One exception to this pattern was in the Santa Barbara Basin where the OMZ was 70 m shallower in 2001–05 compared to 1951–55 (fig. 7). The pattern of the isopleths in both periods shows that the OMZ "intensification" has been driven from the south.

Trends in Prey Fish Abundance

Table 2 describes the relationship between the ten most common fish species reported from the stomachs of jumbo squid in the CCLME (Field et al. 2007) and the ranked abundance of fish larvae averaged over the time period 1954 to 1998 when constrained to the core sampling region of the survey, roughly the SCB. Spatially averaged trends in the abundance of larval fish in the SCB have been highly variable since 1951, but still provide an important indicator of changes in epi- and mesopelagic fish biomass. The species shown in Figure 8 are the six most important fish species in the diet of jumbo squid (Field et al. 2007). The anchovy, hake, and rockfish began to fluctuate and then decline in importance during 1985–90. Sardine began to decline a little later, in about 1998. The mesopelagic fishes *Tarletonbeania crenularis* and *Stenobrachius leucopsarus* have shown no consistent trends in spatially-averaged abundance since 1980.

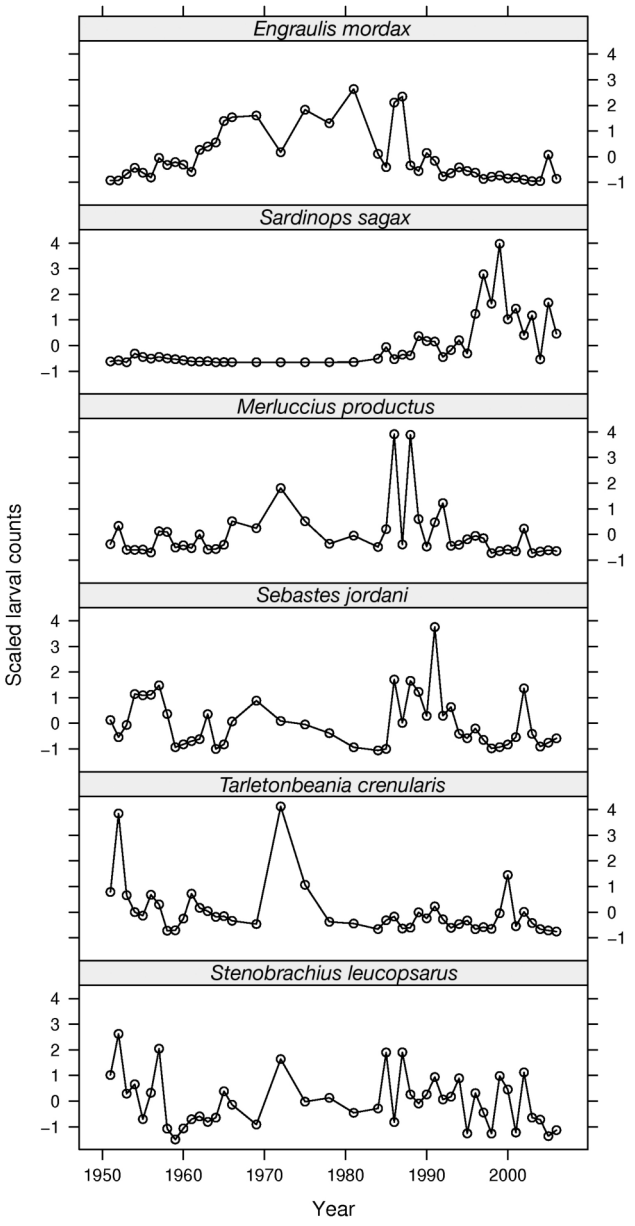

Figure 8. Time series of relative abundances of larval fish sampled with oblique bongo net tows in the Southern California Bight for the years 1950–2006. Data have been scaled and centered to make the series comparable.

DISCUSSION

The results will be discussed as they pertain to the leading hypotheses regarding jumbo squid range expansion: jumbo squid are expanding into the SCB due to top-down effects (a trophic cascade, sensu Myers et al. 2007) caused by reduction in top predators (Zeidberg and Robison 2007) or due to bottom-up effects, climate-linked changes in oceanographic conditions and associated biological changes in prey species (Field et al. 2007; Zeidberg and Robison 2007). To this we add a third mitigating factor: that shoaling of the OMZ may

provide a predation refuge even when highly aerobic predators such as mako sharks are abundant. None of these hypotheses are mutually exclusive.

Predation by Mako Sharks on Jumbo Squid

Like other widely distributed large pelagic predators, mako sharks probably utilize jumbo squid whenever they are abundant. Given the historic presence of jumbo squid off southern Baja and in the GOC where they are an important component of the diet of other large predators (Markaida and Hochberg 2005), it is likely that mako sharks have always consumed jumbo squid while in those waters. We suggest that jumbo squid are not novel prey for mako sharks, rather their persistent availability to mako sharks in the SCB is new. Juvenile mako sharks now have access to jumbo squid throughout their seasonal migration. A number of lines of evidence, photographic and diet, suggest an increase in predation on jumbo squid within the SCB in the last few years.

The JSLS has been conducted most summers since 1994; however, quantitative photographic documentation on the number and extent of squid scars is only now being implemented. Despite a lack of a systematic archive of photographs specifically designed to monitor the presence of scarring, hundreds of photographs from each cruise are available and, based on our observations of these, there is an increase in the extent of scarring on mako sharks in the past two years. The healed nature of many of the marks and the presence of jumbo squid beaks in the stomachs of mortalities sampled during the survey suggest that these encounters are predation events by the mako and not scavenging attacks by the squid occurring once the shark is hooked on the longline.

Additional insights are gained from other studies of mako shark stomach contents, such as the CDGNF stomach sampling program initiated in 2002. As such, if an increase in the occurrence of jumbo squid in the diet of mako sharks occurred as a consequence of the northward expansion of jumbo squid from 1998 to 2002, the stomach sampling program would not capture the change. Mako diet studies for the eastern North Pacific Ocean are scant; however, there is one published study of mako shark diets from the SCB based on five sharks sampled from the CDGNF in 1980 (Mearns et al. 1981) and no jumbo squid were present. In addition, a summary of mako diets based on published and unpublished observations prior to 2002 does not mention jumbo squid as important prey (PFMC 2003). No single diet index is perfect and little is known about differential rates of prey digestion and gut clearance between prey species and between tissue and beaks of jumbo squid. However, the high %FO and GII suggest that mako are deriving a substantial portion of their nutrition from jumbo squid.

To examine the energetic relationship between jumbo squid and mako sharks, we estimated the potential for squid consumption by the locally harvested mako shark population. Based on standard energetic equations and using metabolic rate as a starting point, a mako of the average size taken in the CDGNF (18 kg) can consume 56–113 kg of squid per year, assuming that 25%–50% of their diet is squid. There are certainly limitations to these estimates due to the dearth of data available. One limitation is that the actual relative contribution of squid to the mako shark diet can not currently be estimated due to temporal and spatial limitations in sampling as well as a lack of data on the gut clearance time of beaks. The relative importance of jumbo squid in the mako diet has, however, likely increased in recent years due to the increased habitat overlap between the two species. A second limitation is that many of the metabolic conversions are based on other species and the metabolic rates themselves are extrapolated from a neonate shark. Nonetheless, the associated daily ration estimated in this study (3.4% of body mass per day) is similar to that reported by Stillwell and Kohler (1982) for mako sharks in the northwest Atlantic Ocean (3.2% at 19°C). As expected, this value is higher than for other shark species given the reported high metabolic rate of mako sharks and their regional endothermy (Graham et al. 1990; Sepulveda et al. 2007). For example, the estimated daily ration for blue sharks (*Prionace glauca*), which are not endothermic, is around 1% of body mass (Schindler et al. 2002).

To calculate a minimum estimate of the amount of jumbo squid consumed by mako sharks locally, we applied our energetic estimates to the population of sharks caught annually in the CDGNF. Using the average annual landings from 1982–2006 (163 mt; PFMC 2007), these mako sharks could consume 511 to 1021 mt of jumbo squid per year (tab. 1). The actual consumption of the local population of mako sharks is undoubtedly higher since only a fraction of the population is caught each year; however, abundance estimates are not available to extrapolate consumption to the population level. Other pelagic sharks such as bigeye thresher (*Alopias superciliosus*) and blue sharks are also important jumbo squid predators in the SCB (Preti et al., this volume). Furthermore, additional data are also needed on population estimates for jumbo squid in order to know what percentage of the population is affected by mako and other shark predation.

While overfishing of apex fish predators in the ETP may or may not have an indirect effect on jumbo squid demography and range expansion (Zeidberg and Robison 2007; Watters et al. 2008; Zeidberg and Robison 2008), commercial fishing mortalities in the U.S. West Coast EEZ for mako shark and other known jumbo squid predators, including blue shark, bigeye thresher shark, and swordfish, are much reduced in recent years due to

time-area closures and gear restrictions on longline and gillnet fishing. Most marine mammal predators, such as California sea lion (*Zalophus californianus*), Risso's dolphin (*Grampus griseus*), and sperm whale (*Physeter macrocephalus*), are fully protected and have increasing populations. We conclude that the removal of these top predators is an unproven explanation for the persistence of jumbo squid in the SCB.

Changes in Oxygen and Prey Fish Availability in the CalCOFI Time Series

Secular and episodic changes in temperature are well documented in the CCLME (Roemmich and McGowan 1995; Chavez et al. 2003; Field et al. 2006) and correlations between El Niño and northern range expansions of jumbo squid are well known (Rodhouse, this volume). The thermal tolerance of jumbo squid appears to be quite high and changes in temperature per se do not seem a reasonable explanation for northern range expansion. Jumbo squid can survive at 28°C in surface waters of the GOC (Gilly et al. 2006) and at 1.6°C at a depth of 2000 m in Monterey Bay (Zeidberg and Robison 2007). However, the physiological tolerance of jumbo squid to low oxygen conditions and the potential role of expansion of low oxygen waters in defining squid habitat has only recently been documented (Gilly et al. 2006). Studies to the north (Zeidberg and Robison 2007) and south (Gilly et al. 2006) suggest that jumbo squid probably routinely exploit a vertical niche from the surface to the upper portion of the OMZ. In Monterey Bay, the OMZ begins around 600 m and ends around 1100 m (Vetter et al. 1994; Vetter and Lynn 1997). In Monterey Bay, squid have most commonly been observed at 500 to 600 m, but a small number were observed below the OMZ at depths of 2000 m (Zeidberg and Robison 2007). In the GOC, the 0.5 ml O_2/L isopleth occurs at a depth of slightly less than 200 m in the region of jumbo squid tag deployments (Gilly et al. 2006). In both locations, long-term records of OMZ depth are incomplete or unavailable, so temporal correlations between changes in the OMZ and jumbo squid habitat are only beginning to be considered.

In the SCB, the depth of the OMZ varies from south to north and from inshore to offshore. Basins with limited circulation, such as the Santa Barbara Basin, have a shallower OMZ than the SCB as a whole. Analysis of the CalCOFI record presented here indicates there has been a shoaling in the depth of the OMZ between the initial period of CalCOFI sampling, 1951–55, and recent times, 2001–05. The Santa Barbara Basin and a region in the southern portion of the SCB have experienced the greatest shoaling of the OMZ, but changes have also occurred throughout the core of the CalCOFI pattern. Shoaling of the OMZ on the inner shelf has also recently been reported off Oregon (Grantham et al. 2004; Chan et al. 2008). A more detailed examination of changes in the OMZ is underway, but preliminary examination of the temporal changes at key stations within the SCB does not suggest that there has been a dramatic change in the depth of the OMZ that temporally corresponds with either the 1998 pulse or the 2003 to present range expansion of jumbo squid (McClatchie, unpubl. data).

Within its core range, there have been numerous diet studies that clearly indicate that jumbo squid are opportunistic, generalist feeders that exploit a wide variety of epipelagic and mesopelagic fishes, cephalopods, and pelagic crustaceans (Wormuth 1976; Nesis 1983; Ehrhardt 1991; Nigmatullin et al. 2001; Markaida and Sosa-Nishizaki 2003; Markaida et al., this volume). In the GOC, jumbo squid diet contains a high incidence of myctophid fishes typical of the deep scattering layer (DSL; Markaida and Sosa-Nishizaki 2003) and the OMZ. It has been speculated that an increase in hypoxic habitat has led to an increase in mesopelagic fishes and subsequently jumbo squid have colonized and persisted in the SCB (Weiss[1]).

To examine the potential for bottom-up dietary effects associated with the shoaling of the OMZ, we compared the squid's diet in the CCLME (Field et al. 2007) to changes in the abundance of epi- and mesopelagic fish species as reflected in the CalCOFI ichthyoplankton database. Given that the rankings of larval fish abundance are from more than 50 years of data and represent 301 of the most common fish taxa in the CalCOFI ichthyoplankton database, the correspondence between jumbo squid diet and fish abundance is striking and suggests that the jumbo squid in the SCB are generalists capable of consuming a wide variety of the most abundant epi- to mesopelagic fishes as they vertically migrate throughout the day and night. The ichthyoplankton abundance records for the six most common prey fishes break down into two epipelagic species (sardine and anchovy), two midwater generalists (hake and shortbelly rockfish), and two midwater (or DSL-associated) specialists (northern lampfish and blue lanternfish). An examination of the standardized changes in abundance over the past 56 years shows a number of interesting patterns that in some cases reflect climate changes at ENSO or PDO (Pacific Decadal Oscillation) scales of variation, and in some cases reflect the added effects of fishing and recovery of Pacific sardine (Moser et al. 2001). As with the OMZ record, there was not a clear signal that suggests that an individual species or group of species has changed abundance in a way that coincides with the re-

[1]K. R. Weiss. 2008. "Oxygen poor ocean zones are growing." Los Angeles Times. 2 May 2008.

cent range expansion of the jumbo squid. Further work needs to be done, but this cursory examination of the physical oceanography and prey fish abundances does not point to an anomaly that reflects, in a simple way, the timing of jumbo squid range expansion.

Vertical Niche Overlap of Mako and Jumbo Squid

Based on electronic tagging data from the present and previous studies (Holts and Bedford 1993; Klimley et al. 2002; Sepulveda et al. 2004), makos in the SCB primarily exist within the top 200 m of the water column and exhibit greater vertical activity during daytime hours. Sepulveda et al. (2004) identified feeding episodes by monitoring changes in visceral temperature in free-ranging sharks. For animals tagged between June and November 2002, the majority of feeding events occurred during daylight hours at depths exceeding 100 m. Two other studies of makos tracked in the SCB revealed movements restricted to the top 50 m with no clear diel pattern (Holts and Bedford 1993; Klimley et al. 2002); however, tracking times were limited to 38 hours or less following capture and release. In the Atlantic Ocean, makos demonstrate similar diel behavior patterns of utilizing more of the water column during the day. Makos tracked in the vicinity of the Gulf Stream had a much greater depth range, reaching daytime depths of 400–550 m, although even at those depths water temperatures exceeded 12°C which is greater than temperatures encountered in the current study (Carey et al. 1981; Loefer et al. 2005). The difference in depth likely reflects the deeper thermocline in the Gulf Stream and possibly the larger size of sharks tracked.

For many highly aerobic fish, vertical distribution may be limited by oxygen availability as much as temperature (Randall 1970), and the concept of hypoxia-based niche compression has been developed to explain differences in the vertical distribution of tunas and billfishes in the Atlantic and Pacific Oceans (Prince and Goodyear 2006). Lethal O_2 thresholds based on laboratory studies of swimming performance in skipjack (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) were between 2.16 and 1.14 ml/L (Brill 1994). Prince and Goodyear (2006), based on previous studies (Ingham et al. 1977; Gooding et al. 1981; Bushnell and Brill 1991), considered 3.5 ml O_2/L to be a lower environmental limit for epipelagic billfishes and tunas in their study of hypoxia-based habitat compression. However, recent information from archival tagging indicates that many highly aerobic tuna and billfish species, such as bigeye tuna (*Thunnus obesus*), yellowfin tuna, and swordfish, are capable of occasional deep vertical excursions that can expose them to oxygen concentrations below 1.5 ml/L (Schaefer and Fuller 2002; Brill et al. 2005; Schaefer et al. 2007).

CalCOFI oceanographic data, overlapped with the mako tracks in this study, show that the mako sharks encountered O_2 levels near the thresholds proposed for tunas and billfishes. Mako1 dove to below the 1.5 ml O_2/L isopleth while foraging in Santa Monica Bay, yet never reached the same low O_2 levels while diving offshore where the OMZ was deeper (fig. 6a,b). The data collected to date on vertical movements reveal that mako sharks in the SCB appear to remain primarily above 300 m, 10°C, and 1.5 ml O_2/L (Bedford 1993; Holts and Klimley et al. 2002; Sepulveda et al. 2004; Kohin et al., unpubl. data). The vertical niche overlap between makos and jumbo squid remains to be determined pending archival tagging studies of squid in the SCB, but based on studies from Monterey Bay and the GOC it is likely that there is an area of high contact from the surface to about 300 m and perhaps a predation refuge between 300 m and the limits of hypoxia tolerance of the squid (conservatively the 0.5 ml O_2/L isopleth).

CONCLUSIONS

These results clearly indicate that mako sharks are utilizing jumbo squid as a major diet item in the CCLME. Relative to predators such as the sperm whale, tunas, and swordfish, pelagic sharks are somewhat overlooked and need to be better accounted for in the trophodynamics of jumbo squid and their impact on the CCLME. Better estimates of squid and squid predator abundances are clearly needed, but increased fishing restrictions, including time and area closures of the CDGNF due to leatherback turtle conservation, do not point to an increase in pelagic shark mortality within the U.S. West Coast EEZ. In addition, the population trends of most marine mammal predators are increasing or stable in the CCLME. At this time we conclude that top-down effects are not well supported. The idea that climate changes have produced favorable habitat may be true as there does appear to be an expansion of low oxygen equatorial waters in the SCB. However, it is unclear if jumbo squid favor low oxygen or simply tolerate it. Tolerance of low oxygen does appear to provide a partial refuge for jumbo squid from mako sharks. However, the diet of jumbo squid and their presence in the diet of mako sharks indicate that jumbo squid spend extensive periods of time in the oxygenated surface waters of the SCB. Finally, we were unable to find a simple temporal correlation between changes in oxygen, the abundances of the six most common squid prey fish, and the increase of jumbo squid in the SCB. A more detailed examination of water mass properties is in progress.

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JUMBO SQUID (*DOSIDICUS GIGAS*) BIOMASS OFF CENTRAL CHILE: EFFECTS ON CHILEAN HAKE (*MERLUCCIUS GAYI*)

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ABSTRACT

Jumbo squid (*Dosidicus gigas*) off central Chile (32°00'S–41°30'S) was estimated using data collected from July to November during 2005 and 2006 on board the commercial bottom trawl fleet, where *D. gigas* is part of the bycatch. A geostatistical approach was applied to estimate the jumbo squid biomass in Chilean hake (*Merluccius gayi*) fishing grounds, which reached almost 135,000 t in 2005 and 131,000 t in 2006. The consumption-biomass ratio and the diet composition from a jumbo squid predation study during 2005 and 2006 were used to estimate the consumption of *Merluccius gayi* by *D. gigas* between 2001 and 2006. Assuming a direct relationship between the biomass and the catch per unit effort, *D. gigas* biomass and its consumption were estimated for 2001 to 2004. We also consider that the predation of jumbo squid on Chilean hake played an important role in the biomass reduction of this species off central Chile.

INTRODUCTION

The jumbo squid (*Dosidicus gigas*, d'Orbigny 1835), called "jibia" in Chile and "pota" in Peru, is one of the most abundant squid in the Eastern Pacific Ocean (Nesis 1970; Nigmatullin et al. 2001; Anderson and Rodhouse 2001; Argüelles et al. 2001; Ibáñez and Cubillos 2007) and is one of the largest marine invertebrates of the Chilean fauna (Schmiede and Acuña 1992; Fernández and Vásquez 1995). The geographic distribution of *D. gigas* extends from approximately 40°N to 42°S in the Eastern Pacific Ocean (Wormuth 1998; Nigmatullin et al. 2001), in both oceanic and neritic waters, and from the surface down to depths of 1,200 m (Nesis 1970; Roper et al. 1984; Fernández and Vásquez 1995; Markaida and Sosa-Nishizaki 2001; Nigmatullin et al. 2001; Tafur et al. 2001; Taipe et al. 2001). This species typically lives in areas of high productivity and is most often concentrated in coastal waters from 25°–30°N to 25°–30°S, but in 2004 jumbo squid were confirmed to have been caught as far north as Alaska (57°N) (Hatfield and Hochberg 2007), and in the south near Chiloe island (43°00'S) in 2006.

Like most cephalopods, jumbo squid are characterized by rapid growth and short life spans, and typically reach 120–150 cm of dorsal mantle length (DML) (Lipiński and Underhill 1995; Argüelles et al. 2001; Tafur et al. 2001; Taipe et al. 2001). Nesis (1983) reported that jumbo squid can reach large sizes of up to 360 cm in total length (up to 200 cm in DML) and up to 150 kg in weight, however, Clarke and Paliza (2000) suggest that those sizes could be exaggerated because the maximum dimensions they recorded from specimens found in sperm whales' stomachs caught off Peru had dorsal mantle lengths of 120 cm and body weights of 58–65 kg.

In Chile, most of the existing literature available on *D. gigas* describes the length structure and reproductive activity, the strandings that have occurred in coastal areas, and/or the sporadic and short-term pulses in abundance that can be deduced from the catch records (Wilhelm 1951; Schmiede and Acuña 1992; Fernández and Vásquez 1995; Rocha and Vega 2003; Chong et al. 2005).

The existence of *D. gigas* invasions along the Chilean coast during the 19th century is well-documented. Alcides d'Orbigny, a French naturalist who visited South America at the beginning of the 19th century, wrote in his monumental 1834 work, "Voyage dans l'Amerique Méridionale," that high abundances of *D. gigas* in Chile occurred between Arica (18°20'S) and Valparaíso (33°01'S) during the summer of 1830 (Wilhelm 1930). Wilhelm (1930) reported events of high abundance of *D. gigas* off the central part of Chile, and related those high abundances to the impressive jumbo squid beachings at the end of the summer of 1930 in Concepción Bay (36°41'S–73°02'W). Jumbo squid was abundant off Chile between 1992 and 1994 (Schmiede and Acuña 1992; Arancibia et al. 2007)[1], and since 2001, a new period of high abundance has occurred, with total catch reaching 297,000 t in 2005 (SERNAPESCA 2006, Anuario Estadístico de Pesca 2005. http://www.subpesca.cl).

[1]Arancibia, H., M. Barros, S. Neira, U. Markaida, C. Yamashiro, L. Icochea, C. Salinas, L. Cubillos, Ch. Ibáñez, R. León, M. Pedraza, E. Acuña, A. Cortés, and V. Kesternich. 2007. Informe Final Proyecto FIP 2005-38. Análisis del impacto de la jibia en las pesquerías chilenas de peces demersales. Universidad de Concepción/Universidad Católica del Norte, 299 pp. + Anexxes.

D. gigas are characterized by a complex size structure, high fecundity, sexual dimorphism, and a differentiated sexual ratio (Markaida 2001; Markaida et al. 2004). On the other hand, food habit studies indicate that these animals prey on a number of stocks of commercial and ecological importance in the central part of Chile, including Chilean hake (*Merluccius gayi*), jack mackerel (*Trachurus murphyi*), Chilean common sardine (*Strangomera bentincki*), anchovy (*Engraulis ringens*), lantern fish (*Hygophum* spp.), rattails (*Coelorhynchus* spp.), rockfish (*Helicolenus lengerichi*), deepwater cardinalfish (*Epigonus crassicaudus*), and euphausiids (Ulloa et al. 2006; Arancibia et al. 2007).

Geostatistics is a relatively young statistics field in which spatially-explicit phenomena are studied (Journel and Huijbregts 1978). Petitgas (1993) defines geostatistics as the application of probability theory to estimates of spatial or regionalized variables. Geostatistics is applied in many fields, especially mineral resources, in order to estimate and simulate regionalized variables (Isaaks and Srivastava 1989; Martínez-Vargas and Ramírez-Garcia 2005). Geostatistics was initially applied to fisheries data in 1985 for biomass estimates (Conan 1985; Gohin 1985) using a technique that had been developed for mineral resource estimation (Rivoirard et al. 2000).

While geostatistics has mainly been applied to mining applications, the generality of the subject and diversity of applications are increasing. It has also been applied to terrestrial issues in hydrology (Bardossy 1992; Gardner et al. 2003), agriculture (Lacaze et al. 1994), and forestry (Lyon et al. 2006), and to marine problems in bathymetry (David et al. 1986), mapping sea surface temperature (Gohin 1989), and estimation of various marine biological resources. Included in this latter class are shellfish (Conan 1985), crustaceans (Loch et al. 1995; Rufino et al. 2004), fish eggs and larvae (Fletcher and Sumner 1999; Bez 2002; Castillo-Jordán et al. 2007), spatial plankton distribution (Bez and Rivoirard 2001; Simard et al. 2003), biomass of fishes (Simard et al. 1993; Petitgas 1993; Maravelias 1999; Barange et al. 2005), and the present subject, squids.

The consumption of Chilean hake by *D. gigas* is considered one of the factors that could explain the recent biomass reduction and the quasi-collapse of the Chilean hake fishery (Arancibia and Neira 2005[1]). But, there are no estimates of jumbo squid biomass with which to assess the total consumption of Chilean hake. The objectives of this work are: (1) to estimate the biomass of *D. gigas* in the fishing grounds of Chilean hake between 2001 and 2006; and (2) estimate the jumbo squid consumption of Chilean hake using consumption-biomass ratio estimates (Q/B) and jumbo squid diet composition (DC) during the same period.

METHODS

Biomass Estimates in 2005 and 2006

To estimate the biomass of *D. gigas* in the study area (fig. 1), density data, measured as catch per unit of swept area (cpua, t/km^2), was collected between July and November in 2005 and 2006 on board commercial bottom trawl vessels from the Chilean hake fishery, between 32°00'S–41°30'S. This study area represents the main distribution area of the Chilean hake fishery.

The total study area was separated into two geographic zones, defined according to the orientation and shape of the coastline and the extension and distribution of the continental shelf (Lillo et al. 2007)[2]. The limit between the geographic zones was arbitrarily fixed at 37°06'S, defining a north area and a south area (fig. 1).

All the data used were collected on board by scientific observers as part of a joint monitoring program between the Chilean hake fishing industry and the Instituto de Investigación Pesquera (INPESCA). The jumbo squid catch was weighed directly on board after being separated from the Chilean hake specimens. *D. gigas* is caught as bycatch in the Chilean hake fishery and the jumbo squid catch is independent of the fishery, which means that the jumbo squid catch can be considered a random sample of its abundance, a condition needed to apply the swept-area method to this species (Godø 1994).

The density (tons/km^2) of jumbo squid in each haul was calculated as:

$$z(x_i) = \frac{C_i}{WS_i \cdot sd_i}, \quad (1)$$

where $z(x_i)$ is the value of the density (tons/km^2) of jumbo squid at x_i, which is the trawl middle point; C_i is the catch (tons) of jumbo squid; WS_i is the wing spread of the net; and sd_i is the swept distance.

The wing spread of each haul used in this study was measured directly on board by the scientific observers, as we only use data from vessels that have electronic devices to measure both wing spread and the vertical spread of the net. At least five measures of the wing spread were taken during the hauls; for each haul the average of those measures were used. The wing spread of the nets fluctuated between 16 and 20 m.

In using the geostatistical approach to estimate the biomass of *D. gigas* in the Chilean hake fishing grounds, the spatial relationship between densities was explored by computing an empirical semivariogram, the basic geostatistics tool (Rivoirard et al. 2000). The empirical var-

[2]Lillo, S., R. Bahamonde, J. Olivares, J. Saavedra, E. Díaz, E. Molina, M. Braun, S. Núñez, A. Sepúlveda, R. Alarcón, and A. Saavedra. 2007. Evaluaciones hidroacústicas de merluza común, año 2006. Informe Final Proyecto FIP 2006-03. 597 pp.

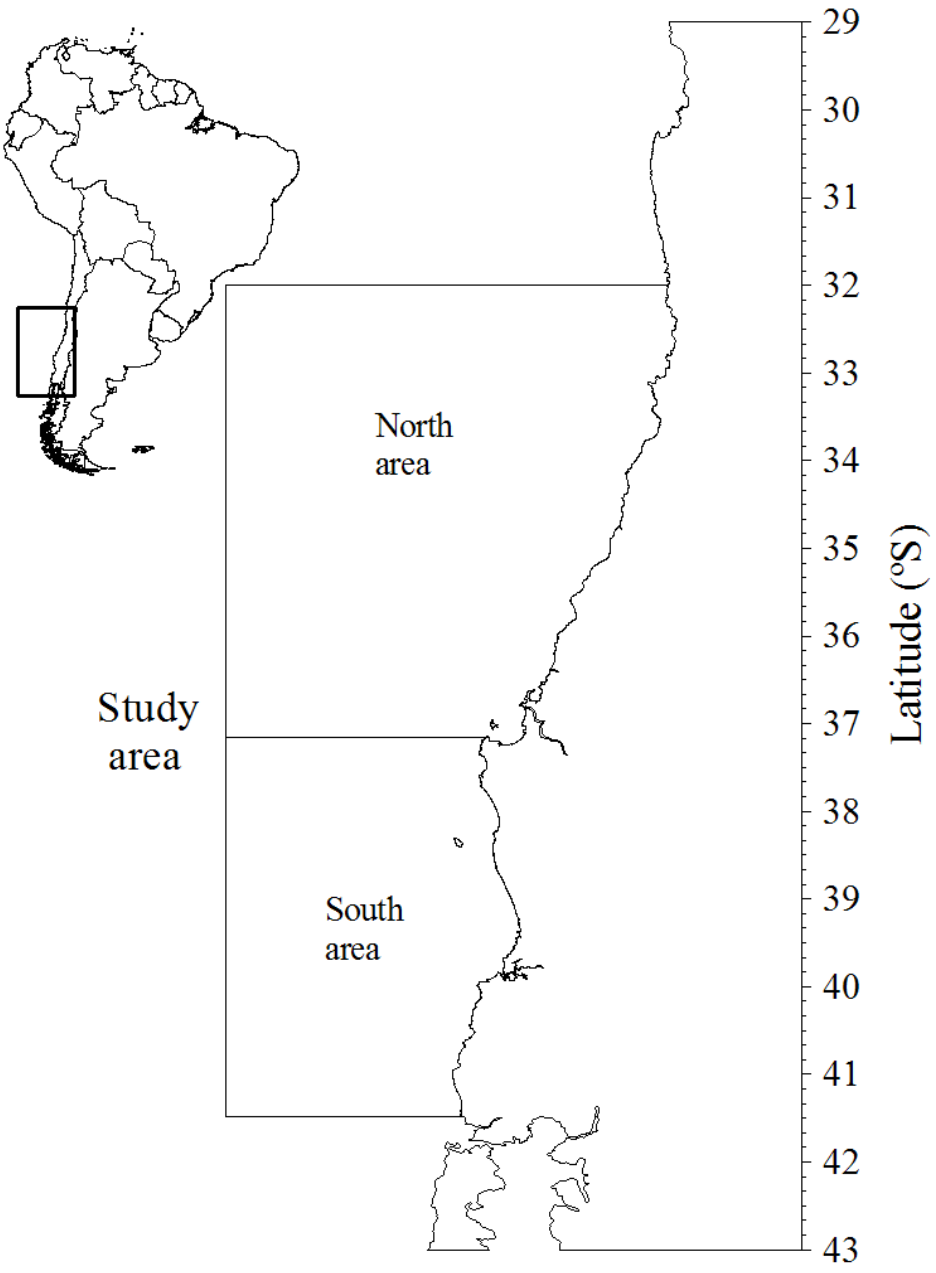

Figure 1. Study area shown separated in two working areas (north and south).

iogram is defined as the variance of difference between values that are h units apart and is a function of variance and covariance, i.e.:

$$\gamma^* = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} \left(z(x_i) - z(x_i + h)\right)^2, \quad (2)$$

where h is a vector of distance and direction, and $N(h)$ is the number of pairs of observations at distance h and a given direction. However, we also chose the robust (or stable) variogram estimator (Cressie and Hawkins 1980; Cressie 1993) since it permitted a better definition for the variogram pattern for the spatial distribution of *D. gigas* densities (Sullivan 1991):

$$\gamma^* = \frac{\left(\sum_{i=1}^{N(h)} \left(z(x_i) - z(x_i + h)\right)^{\frac{1}{2}} \right)^4}{2N(h)^4 \left(0.457 + \frac{0.494}{|N(h)|}\right)}. \quad (3)$$

In the present analysis, second-order stationarity was assumed (Journel and Huilbregts 1978), where the following applied: (1) the mathematical expectation (or

mean) of the random function, $E(Z(x))$, is independent of the support point x; and (2) for each pair of regionalized variables $(z(x_i) - z(x_i + h))$ the covariance, C, is independent of the separation distance, h (Matheron 1971; Journel and Huilbregts 1978). The stationarity of the covariance implies the stationarity of the semivariogram (Journel and Huilbregts 1978). In order to explore and to detect whether the intensity of spatial autocorrelation varies according to direction (anisotropic process), experimental semivariograms were calculated in four directions (0°, 45°, 90°, and 135°).

To characterize the spatial structure of the *D. gigas* density, three mathematical models were tested: the spherical, exponential, and the Gaussian models. These models, in terms of the semivariogram, are described in Cressie (1993):

$$\gamma(h;\theta) = \begin{cases} 0, & h = 0 \\ c_0 + c\left(\frac{3}{2}\left(\frac{\|h\|}{r}\right) - \frac{1}{2}\left(\frac{\|h\|}{r}\right)^3\right), & 0 < \|h\| \le r \\ c_0 + c, & \|h\| \ge r \end{cases} \tag{4}$$

for the spherical model,

$$\gamma(h;\theta) = \begin{cases} 0, & h = 0 \\ c_0 + c\left(1 - \exp\left(-\frac{\|h\|}{r}\right)\right), & h \neq 0 \end{cases} \tag{5}$$

for the exponential model, and

$$\gamma(h;\theta) = \begin{cases} 0, & h = 0 \\ c_0 + c\left[1 - \exp\left(-\frac{3\|h\|^2}{r^2}\right)\right], & h \neq 0 \end{cases} \tag{6}$$

for the Gaussian model, where c is the sill of the variogram that represents the maximum level of variability, r is the range of the variogram beyond which data are no longer autocorrelated, and c_0 is the nugget effect. The models were fitted to the variogram estimates according to an approximate weighted-least-squares (WLS) procedure (Cressie 1993; Pelletier and Parma 1994).

To select the best model and evaluate alternative models for kriging, a cross-validation was performed. In cross-validation analysis, each measured point in a data set is individually removed from the set and its value is then estimated via kriging as though it were never there (Davis 1987). In this way, the prediction error for each sampled locality is defined as the difference between the measured value and the estimated value from the rest of the data (Isaaks and Srivastava 1989). The mean squared deviation ratio (MSDR) of residuals was used as a goodness of fit measure:

$$\text{MSDR} = \frac{1}{n}\sum_{i=1}^{n}\frac{[z(x_i) - \hat{z}(x_i)]^2}{\hat{\sigma}^2(x_i)}, \tag{7}$$

where $\hat{\sigma}^2(x_i)$ is the kriging variance at cross-validation point x_i.

Ordinary point kriging was used as the interpolation method to reproduce the stochastic processes within the distribution regions (loci) of *D. gigas* in the study area. An interpolation grid was imposed into each abundance locus with internodal distance as the average minimum distance between hauls. The abundance region (locus) was defined according to the presence/absence of *D. gigas* in trawls.

Both variogram and kriging parameters were used to estimate the density, $z^*(x_0, y_0)$, of *D. gigas* in the localities (x_0, y_0):

$$z^*(x_0, y_0) = \sum_{i=1}^{n} \omega_i z(x_i, y_i), \tag{8}$$

where ω_i represent the weights for each sampled locality. The sum of the weights is equal to 1.

Inside of each abundance locus, the mean density (z^*_{kg}) was estimated by averaging the local estimates. The biomass of *D. gigas* in each abundance locus $(\hat{B}_j)$, was calculated as:

$$\hat{B}_j = \frac{1}{\bar{a}}\ \hat{S}_j \cdot z^*_{kg}, \tag{9}$$

where $\hat{S}_j$ is the area (km^2) of the j-locus, and $\bar{a}$ is the average local capturability index which, for simplicity, was assumed equal to 1. Then, the total biomass of *D. gigas* is the sum of all abundance regions identified in the study area, i.e.:

$$\hat{B} = \sum_{j=1}^{n} \hat{B}_j. \tag{10}$$

Jumbo Squid Biomass Between 2001 and 2004

We established that no direct estimates of jumbo squid biomass between 2001 and 2004 existed. Then, with annual *D. gigas* CPUE (tons by sweep hour, t/sh) from 2001 to 2006 (fig. 2), and the direct relationship between CPUE and biomass (Sparre and Venema 1997),

$$\text{CPUE} = q \cdot B, \tag{11}$$

the capturability coefficient (q) was obtained separately for 2005 and 2006, as was the two-year average ($\bar{q}$). With this average capturability coefficient, and the annual CPUE data, *D. gigas* biomass was calculated for 2001 to 2004, according to the following expression:

$$\hat{B}_\gamma = \frac{\text{CPUE}}{\bar{q}}. \tag{12}$$

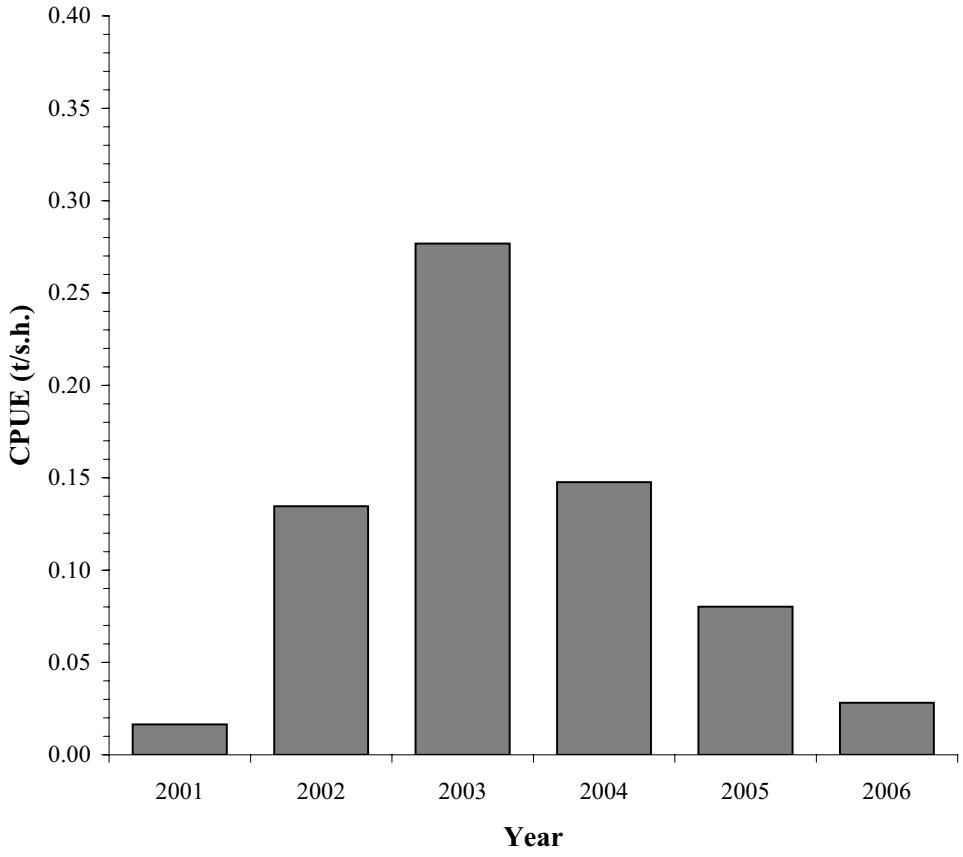

Figure 2. Annual catch per unit effort (tons by sweep hour, t/s.h.) of jumbo squid (*Dosidicus gigas*) off central Chile between 2001 and 2006.

Consumption of Chilean Hake

To estimate Chilean hake consumption (Q_i) by *D. gigas*, three parameters have to be known: (1) the biomass of the predator (B_j), (2) the consumption-biomass relationship of the predator $(Q/B)_j$, and (3) the diet composition (DC_{ij}) of the prey (i) in the stomach contents of the predator (j). The expression to calculate the consumption is:

$$Q_i = \sum_{i=1}^{n} B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ij} . \qquad (13)$$

RESULTS

From analysis of positive and negative trawls (zero catch) for *D. gigas*, ten abundance foci were identified in 2005, and thirteen in 2006 (fig. 3), covering 19,346.7 km² and 12,695.5 km², respectively (tab. 1).

The analysis of directional variograms showed differences in the spatial autocorrelation between both years and areas. Therefore, a directional variogram was calculated for each area, except in the south area for 2006 where an omni-directional variogram was adjusted. In all cases, the spherical model showed the best fit (fig. 4). The range of the variogram fluctuated between 11.2 km in the south area in 2005 and 19.0 km in the north area in 2006 (tab. 2).

D. gigas biomass in the Chilean hake fishing grounds estimated through the geostatistic method reached more

TABLE 1
Number of biomass loci of *Dosidicus gigas* identified in the study area in 2005 and 2006, the coverage area (km²), and the biomass (t) estimated in each locus and total.

	2005		2006	
Locus	Area (km²)	Biomass (t)	Area (km²)	Biomass (t)
1	278.7	2,577.5	293.0	3,680.0
2	182.4	2,332.0	392.8	6,954.0
3	563.2	2,630.5	170.4	2,076.0
4	677.8	3,072.0	163.5	5,724.5
5	5,956.8	45,627.0	1,987.1	17,604.5
6	779.2	7,380.5	2,290.0	14,259.0
7	63.7	641.5	292.5	8,008.5
8	2,755.9	27,104.5	93.6	767.5
9	3,718.6	17,016.0	545.9	5,980.0
10	4,370.4	26,291.0	93.5	868.5
11	—	—	569.3	11,973.5
12	—	—	2,008.5	21,090.0
13	—	—	3,795.4	32,200.5
Total	19,346.7	134,672.5	12,695.5	131,186.5

Figure 3. Spatial localization of the biomass loci of jumbo squid (*Dosidicus gigas*) off central Chile in 2005 (A: north area; B: south area), and 2006 (C: north area; D: south area). In parenthesis appears the number of the locus.

TABLE 2
Parameters of the spherical variogram model fitted to the empirical variogram for the spatial distribution of the density of *Dosidicus gigas* off central Chile in 2005 and 2006. RSS = Residual Sum of Squares.

	2005		2006	
Parameter	North area	South area	North area	South area
Range (km)	11.639	11.169	18.966	12.174
Sill	0.242	0.345	0.368	1.306
Nugget	0.445	0.360	0.176	0.545
RSS	0.072	0.098	0.105	2.082

than 134,000 t in 2005 and almost 131,000 t in 2006. Then, using equation 11 we estimate the catchability coefficient for 2005 and 2006 as equal to 4.054×10^{-7} (tab. 3).

To estimate the annual total biomass of *D. gigas*, it is necessary to add together the corresponding landings from the same area and year. Thus, *D. gigas* landings for the study area were 213,393.0 t in 2005 and 180,355.0 t in 2006. Therefore, the annual biomasses of jumbo squid in 2005 and 2006 were 348,065.5 t and 311,541.5 t, respectively (tab. 3).

Once the catchability coefficient and CPUE were determined, we used equation 12 to calculate the annual biomass of *D. gigas* as more than 680,000 t in 2003 and almost 40,000 t in 2001. According to official landings, there is no evidence of high jumbo squid abundance off central Chile, since at least five years before 2001. Finally, with the biomass estimate and the consumption-biomass relationship (Q/B) for *D. gigas* ($Q/B = 5.3$), and the diet composition (DC) of Chilean hake in the stomach contents of the predator ($DC = 15\%$), parameters taken from Arancibia et al. (2007), the annual hake consumption was estimated for the years 2001 to 2006 as more than 500,000 t in 2003 (tab. 3).

DISCUSSION

Since December 2001, jumbo squid have been found in relatively high abundances in both the purse seine and bottom trawl fleet catches off the central-south coast of Chile. These high abundances were apparently due to the reproductive success of the species, associated with cold oceanographic conditions that occurred in 1999 and 2000, after the El Niño event of 1997–98 (Cubillos et al. 2004)[3]. The increase in the relative abundance of *D. gigas* resulted in the species being found both in the oceanic and coastal sector from August 2003 and January 2004 (fig. 5), with captures fluctuating between a few kilos to almost 100 t per haul.

Nevertheless, in spite of the increase in the presence of jumbo squid in the industrial and artisan captures reflected in the landings as 15,000 t in 2003, 296,000 t in 2005, and 210,000 t in 2006 (SUBPESCA 2007, www.subpesca.cl), biomass estimates of the resource do not exist for that period, except in the recent work of Arancibia and Neira (2007). They estimated the jumbo squid biomass for 2005 at 400,000 t using an ECOPATH model, which is not significantly different from our estimate of nearly 348,000 t (tab. 3).

Arancibia and Neira (2007), using the same ECOPATH model, estimate Chilean hake consumption by jumbo squid for the same year that they estimate the jumbo squid biomass (2005). Chilean hake consumption was calculated to be 300,000 t, which is comparable to our estimate of almost 277,000 t (tab. 3).

Concurrent with the increase in jumbo squid abundance off central Chile was a reduction in the availability/abundance of traditional fishing resources such as Chilean hake, Chilean hoki (*Macruronus magellanicus*), and cardinal fish (*Epigonus crassicaudus*)(Arancibia et al. 2007). Before 2002, the Chilean hake fishery was considered healthy with a robust population structure, stable average weights at age, and an increasing trend in abundance (Lillo et al. 2007, tab. 4).

Reduction in Chilean hake abundance during 2004–06

[3]Cubillos, L., Ibáñez Ch., González C., and A. Sepúlveda. 2004. Pesca de Investigación: Pesca de Jibia (*Dosidicus gigas*) con red de cerco entre la V y X Regiones, año 2003 (Research Fishery: Catch of Jumbo flying squid (*Dosidicus gigas*) with purse seine between V and X Region, Year 2003). Inst. Inves. Pesq. VIII Región. Talcahuano (Chile): pp.1–48.

TABLE 3
Annual CPUE (tons per sweep hour, t/s.h.) of jumbo squid (*Dosidicus gigas*), capturability coefficient (q), estimate of jumbo squid biomass in Chilean hake (*Merluccius gayi*) fishing grounds (B_{fg}, tons), *D. gigas* landings, estimate of annual biomass of *D. gigas* off central Chile, and estimated consumption of *M. gayi* by *D. gigas* between 2001 and 2006.

Year	CPUE (t/s.h.)	q	B_{fg} (t)	Landings (t)	Annual Biomass (t)	Consumption of Chilean hake (t)
2001	0.016				40,440.3	32,150.1
2002	0.135				331,878.8	263,843.6
2003	0.277				682,646.5	542,704.0
2004	0.148				364,139.3	289,490.7
2005	0.080	5.959×10^{-7}	134,672.5	213,393.0	348,065.5	276,712.1
2006	0.028	2.148×10^{-7}	131,186.5	180,355.0	311,541.5	247,675.5
		Average = 4.054×10^{-7}				

TABLE 4
Biomass (tons) of *Merluccius gayi* estimated in acoustics surveys made between 1995 and 2006 in central Chile (Lillo et al. 2007).

Year	Biomass (t)
1995	505,765
1997	712,878
1999	899,307
2000	891,598
2001	917,133
2002*	1,555,422
2004	273,860
2005	222,721
2006	266,596

*This value of biomass is considered highly overestimated.

has been attributed to three important factors: (1) a high predation of Chilean hake by jumbo squid (Arancibia and Neira 2005); (2) a high degree of cannibalism (Jurado-Molina et al. 2006); and (3) overestimation of the stock size in 2002 that relates to high capture quotas (Arancibia and Neira 2006).

Before 2007, the true impact of jumbo squid predation on Chilean hake was very difficult to determine because absolute abundance of the predator as well as basic aspects of its feeding biology were not known. In that sense, the biomass estimates made within the framework of this study and the estimates of the consumption-biomass ratio (Q/B) calculated by Arancibia et al.

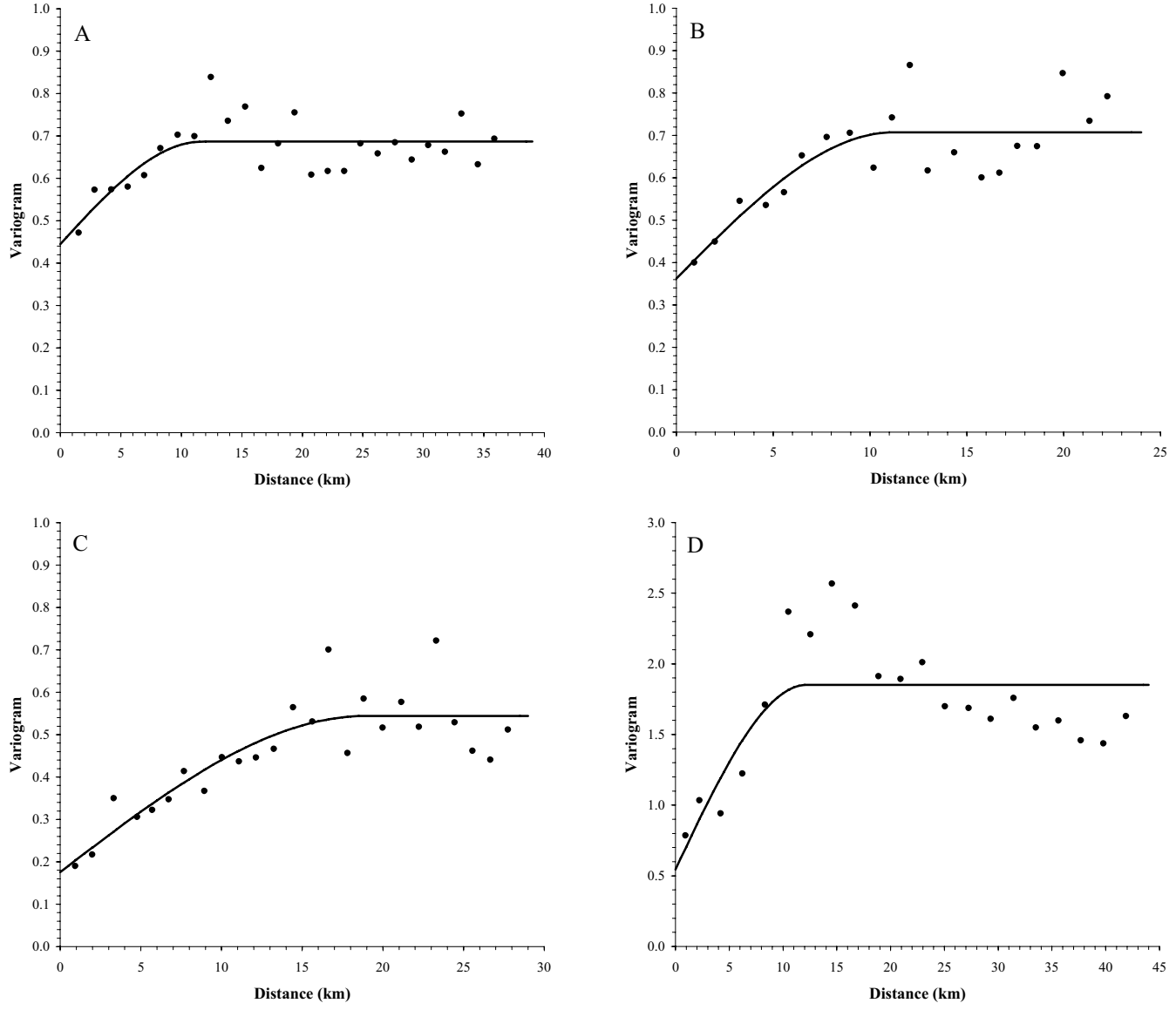

Figure 4. Theoretical variogram (black line, spherical model) adjusted to the empirical variogram (black dots) for the spatial distribution of the density of jumbo squid (*Dosidicus gigas*) in central Chile in 2005 (A: north area; B: south area), and 2006 (C: north area; D: south area).

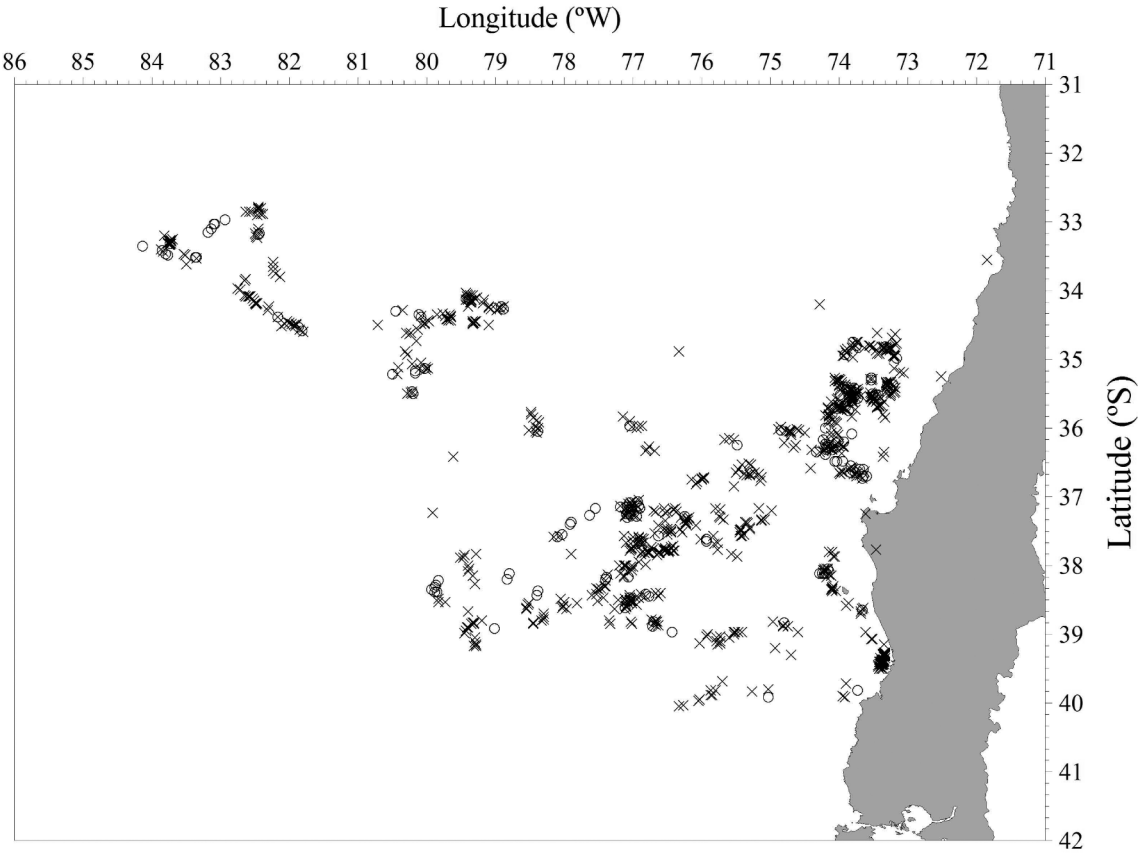

Figure 5. Spatial distribution of hauls with presence of *Dosidicus gigas* (o, white points) in the industrial Jack mackerel (*Trachurus murphyi*) purse seine fisheries off central Chile between August 2003 and January 2004. Crosses (x) are hauls without jumbo squid.

(2007), both used to estimate the consumption of Chilean hake by jumbo squid, allow us to conclude that jumbo squid predation on Chilean hake played an important role in the reduction of its biomass.

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ECOLOGY AND DISTRIBUTION OF THE NORTHERN SUBPOPULATION OF NORTHERN ANCHOVY (*ENGRAULIS MORDAX*) OFF THE U.S. WEST COAST

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ABSTRACT

Northern anchovy (*Engraulis mordax*) are a dominant fish in the northern California Current and are important prey for many predators. However, little is known about how anchovy distribution and abundance are affected by oceanographic variability in the eastern Pacific Ocean. We examined the relationship between anchovy abundance and environmental variables at two spatial and temporal scales: mesoscale (surface temperature, salinity, density, chlorophyll *a*, distance from shore, and depth) and macroscale (Pacific Decadal Oscillation Index, Multivariate El Niño-Southern Oscillation Index, timing of the spring transition to upwelling conditions, and abundance of cold-water zooplankton). Anchovy densities increased significantly from 1999–2004, and decreased significantly from 2005–06 in conjunction with delayed coastal upwelling and decreases in the overall abundance of cold-water zooplankton. Sea surface temperatures and proximity to the shore explained most anchovy abundance and distribution variations. When lagged by one year, a northern copepod biomass anomaly strongly correlated to age-1 anchovy survival, suggesting that copepod abundance may determine year-class strength.

INTRODUCTION

Northern anchovy (*Engraulis mordax*; anchovy) often dominate pelagic nekton biomass in the California Current, along with a few other forage species, including Pacific sardine (*Sardinops sagax*) (Brodeur et al. 2005; Emmett et al. 2005). The northern subpopulation of northern anchovy ranges from Eureka, California, to the Queen Charlotte Islands, British Columbia, Canada (McHugh 1951), and supports a small bait fishery centered off the Columbia River. Live anchovy are captured in purse seines and sold to commercial and recreational fishermen targeting Pacific hake (*Merluccius productus*), coho (*Oncorhynchus kisutch*) and chinook (*Oncorhynchus tshawytscha*) salmon. The Department of Fisheries and Oceans Canada (DFO) closed the anchovy fishery off western Vancouver Island in 2002 because the small fishery could not pay for a stock assessment.

Previous investigations have revealed correlations between California Current climate changes and forage fish regime shifts (Baumgartner et al. 1992; Schwarzlose et al. 1999; Rodriguez-Sanchez et al. 2002; Chavez et al. 2003), yet no studies provide information about the distribution of the northern subpopulation of northern anchovy in relation to local and basin-wide changes in climate or the marine ecosystem. In this study, we explored spatial and temporal patterns of distribution of the northern subpopulation of northern anchovy in the California Current Large Marine Ecosystem (CCLME) from 1977–2006 using data from National Marine Fisheries Service (NMFS) time-series sampling efforts off Oregon and Washington. In particular, we tested the hypothesis that anchovy abundance is linked to cool ocean conditions by examining catch of the northern subpopulation of northern anchovy with reference to *in situ* physical oceanographic conditions in the eastern Pacific Ocean.

In addition to spatial and temporal patterns of distribution and abundance, biological parameters of interest to this study include anchovy size and age composition (from length and otolith analysis) over time and space. Our results provide ecological information about the northern subpopulation of northern anchovy relevant to ecosystem-based fishery management of the CCLME.

METHODS

Commercial Catch Information

Commercial catch data for northern anchovy from 1985–2006 in the Pacific Northwest were obtained from the Oregon Department of Fish and Wildlife (ODFW), the Washington Department of Fish and Wildlife (WDFW), and the Department of Fisheries and Oceans (DFO) Canada. These data represent time-series catch information from the purse seine fishery targeting anchovy as live bait, without a metric for effort.

Distribution and Abundance

Catch data from four separate fishery-independent studies conducted by NMFS through either the Northwest Fisheries Science Center (NWFSC) or the Alaska Fisheries Science Center (AFSC) from 1977–2006 were mapped geographically (tab. 1, fig. 1). All stations were not sampled equally in all years in a given study. With the exception of the Triennial Study, described more fully in Emmett and Brodeur (2000), all investigations targeted coastal pelagic species. We extracted data from recorded measurements of anchovy abundance and size (fork lengths [FL] in mm), as well as detailed oceanographic information relating to anchovy environment.

The first of the four studies, the AFSC West Coast Triennial bottom trawl study (Triennial Study), began in 1977 and was repeated every three summers (June–August) until 2004. Anchovy caught during these surveys were incidental by-catch, likely trapped in the bottom trawl gear in mid-water during deployment and retrieval of the nets. Anchovy were counted, measured, and weighed from each haul (data courtesy of M. Wilkins, NMFS, AFSC, Seattle, WA). We include only samples caught between 42° and 48°N latitude, that overlap spatially with our target surveys, although anchovy were captured as far south as 32°N latitude, off southern California.

The other three studies were conducted by the NWFSC. From 1998–2006, the NWFSC monitored pelagic fish resources off Oregon and Washington using surface trawls in: (1) the Bonneville Power Administration (BPA) Columbia River Plume Study (Plume Study), (2) the U.S. Global Ocean Ecosystem Dynamics (GLOBEC)–Northeast Pacific Study (GLOBEC Study), and (3) the Predator Study (fig. 1). The Plume Study consisted of daytime hydrographic surveys and fish sampling in the Columbia River plume and off the coasts of Oregon and Washington during June and September 1998–2006 (Brodeur et al. 2005), with additional cruises in May 1999–2006, November 2003, and August 2005. The GLOBEC Study consisted of four cruises conducted as part of a mesoscale and fine-scale sampling study within the U.S. GLOBEC Northeast Pacific Program (Batchelder et al. 2002; Reese and Brodeur 2006). Cruises occurred in nearshore (0–100 km) waters between Newport, Oregon, and Crescent City, California, during June and August 2000 and 2002. Stations were designated along transects that had been monitored for several years, and chosen for their proximity to features in the physical environment, such as fronts and eddies (Brodeur et al. 2004). The Predator Study consisted of a series of two-day sampling cruises occurring approximately every ten days associated with the Columbia River plume in 1998, and on two transects north and south of the Columbia River from April to August 1999–2006 (Emmett et al. 2001; Krutzikowsky and Emmett 2005; Emmett et al. 2006). While Plume and GLOBEC Study cruises sam-

TABLE 1

An inventory of all National Marine Fisheries Service (NMFS) cruises used for this paper. The duration of each cruise varied among studies; Predator Study cruises accounted for only two nights of sampling (12 stations total); Triennial Study cruises occurred from June–September and sampled ~600 stations per cruise. All stations depicted were not sampled equally in all years in a given study.

Year	Study	Dates	Area	Trawl Type	Physical data
1977–95	Triennial	June-September, every 3 years	West Coast	Bottom	N
1998	Triennial	June-September, every 3 years	West Coast	Bottom	N
	Plume	6/16-6/25, 9/20-9/29	OR, WA	Surface	Y
	Predator	4/16-8/12, ~ every 10 days	Columbia River	Surface	Y
1999	Plume	5/18-5/25, 6/16-6/24, 9/21-10/1	OR, WA	Surface	Y
	Predator	4/13-7/29, ~ every 10 days	Columbia River	Surface	Y
2000	Plume	5/22-5/24, 6/17-6/25, 9/19-9/24	OR, WA	Surface	Y
	Predator	4/29-7/24, ~ every 10 days	Columbia River	Surface	Y
	GLOBEC	5/29-6/11, 7/28-8/12	Southern OR	Surface	Y
2001	Triennial	June-September, every 3 years	West Coast	Bottom	N
	Plume	5/20-5/28, 6/24-7/2, 9/21-9/29	OR, WA	Surface	Y
	Predator	4/25-8/1, ~ every 10 days	Columbia River	Surface	Y
2002	Plume	5/21-5/29, 6/21-6/28, 9/20-10/3	OR, WA	Surface	Y
	Predator	4/23-8/3, ~ every 10 days	Columbia River	Surface	Y
	GLOBEC	6/1-6/18, 8/1-8/17	Southern OR	Surface	Y
2003	Plume	5/20-5/27, 6/23-7/3, 9/26-10/3, 11/13-11/18	OR, WA	Surface	Y
	Predator	4/23-7/30, ~ every 10 days	Columbia River	Surface	Y
2004	Triennial	June-September, every 3 years	West Coast	Bottom	N
	Plume	5/22-5/29, 6/22-6/29, 9/22-9/29	OR, WA	Surface	Y
	Predator	4/28-8/12, ~ every 10 days	Columbia River	Surface	Y
2005	Plume	5/29-5/31, 6/12-6/22, 8/21-8/27, 9/21-9/28	OR, WA	Surface	Y
	Predator	4/19-8/13, ~ every 10 days	Columbia River	Surface	Y
2006	Plume	5/24-5/30, 6/19-6/28, 9/20-9/28	OR, WA	Surface	Y
	Predator	5/11-8/30, ~ every 10 days	Columbia River	Surface	Y

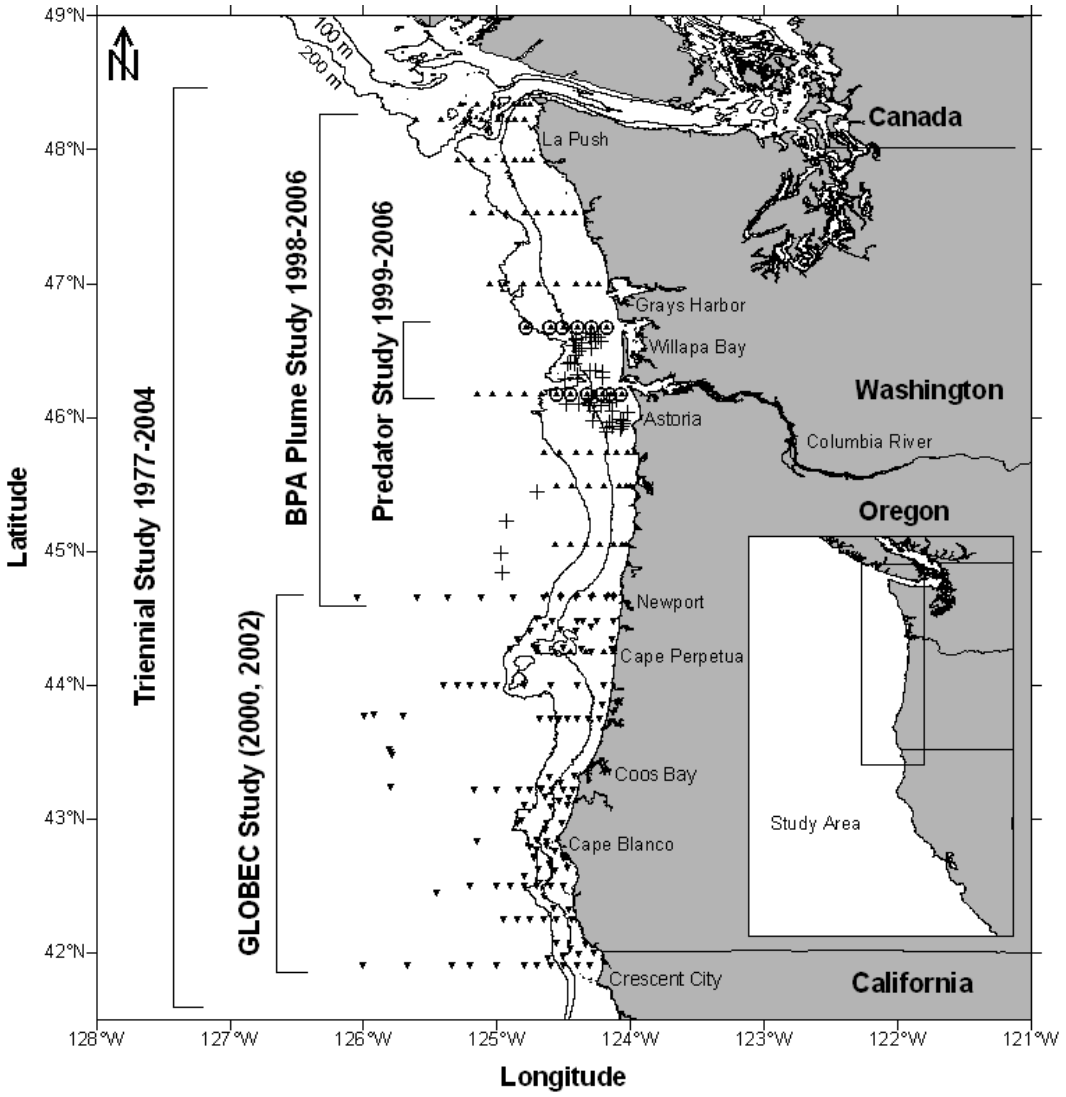

Figure 1. Map showing the four National Marine Fisheries Service (NMFS) pelagic sampling cruise locations (Triennial, Plume, GLOBEC, and Predator Study cruises). Triangles show Plume Study stations, inverted triangles represent GLOBEC Study stations, plus signs designate 1998 Predator Study stations, and open circles show 1999–2006 Predator Study stations. Also shown are the 100 and 200 m depth contours. Sampling efforts varied by year and cruise.

pled during the day or crepuscular periods, the Predator Study cruises sampled entirely at night.

All three of the pelagic fish surveys used a Nordic 264 rope trawl (NET Systems, Bainbridge Island, Washington) fished directly astern the vessel at the surface. The mouth of the trawl measured 12 m deep by 28 m wide (336 m^2), as determined during an early cruise using a third-wire Simrad FS3300 backwards-looking net sounder (Emmett et al. 2004). The trawl had variable mesh sizes (162.6 cm at the mouth to 8.9 cm at the cod end), with an additional 6.1 m long, 0.8 cm knotless liner sewn into the cod end. A pair of 3.0 m wide foam-filled doors spread the mouth apart, and the trawl was towed for 15–30 minutes with approximately 300 m of warp. To keep the net at the surface, two A-4 Polyform floats were tethered to each wing tip and two single floats were clipped on either side of the center of the headrope.

All anchovy captured in each trawl were counted and a random subsample (n = 30 or n = 50) measured for fork length (FL; mm). In the event of a very large catch, we counted and weighed a subsample of anchovy. In these hauls we used the measured weight of the remaining anchovy catch to calculate the total number from the determined number of anchovy/kg. We calculated anchovy density (number of fish/10^6 m^3) by dividing the number of anchovy in a haul by the volume of water the net fished, and by standardizing the density to number per 10^6 m^3. We calculated the volume of water by multiplying the trawling distance (m), identified by GPS, by the effective fishing mouth area (336 m^2).

Habitat Analysis

We collected environmental information immediately before fishing at each station during Predator, GLOBEC, and Plume Studies using a Sea-bird SBE 19 SeaCat conductivity-temperature-depth (CTD) profiler. Measurements of temperature (°C), salinity (psu), and density (σ-θ) were recorded at 1 m depth intervals from the surface to 100 m or 10 m from the bottom. Shifts in the basin-wide oceanographic conditions of the northern California Current ecosystem were assessed by the Pacific Decadal Oscillation (PDO) Index (Joint Institute for the Study of the Atmosphere and the Oceans, http://www.jisao.washington.edu/pdo/), the Multivariate El Niño Southern Oscillation (ENSO) Index (MEI; NOAA-CIRES Climate Diagnostics Center, http://www.cdc.noaa.gov/ENSO), and timing of the spring transition (Huyer et al. 1979; Logerwell et al. 2003) from winter coastal downwelling and poleward winds to spring or summer upwelling and equatorward winds. In addition, we collected chlorophyll *a* from water at 3 m depth on Whatman GF/C glass microfiber filters during Plume and GLOBEC Study cruises. We treated chlorophyll samples with acetone and measured them (µg/L; C) with a Turner Designs 10-AU Fluorometer.

Age Analysis

Anchovy ages were estimated from samples collected during the 2005 Predator Study between April and August. We randomly chose thirty individuals from each of ten hauls (n = 300), of which northern anchovy comprised more than 10% of the total catch. The fish were frozen whole on board the ship (–20°C) and returned to the lab for processing. We recorded FL (mm) and wet weight (to the nearest 0.01g), removed the saggital ototliths according to a protocol previously developed for anchovy otolith extraction (Messersmith 1969), and then cleaned and stored them in 95% ethanol. The otoliths from five fish were unreadable.

We photographed each otolith under a Leica MZ7.5 high-performance stereomicroscope equipped with digital imaging software at 50× magnification. For aging, one reader determined otolith annuli from surface reads, and the median from three reads taken on three separate days was recorded for each fish. We calculated an index of average percent error (APE) (Beamish and Fournier 1981) for all reads and generated a length-frequency age-overlay histogram, which proved useful for detecting year classes.

Data Analysis

All statistical analyses were run using the S-Plus 6.2 software package (Insightful Corp. Seattle, WA). We used a Kruskal-Wallis test to evaluate statistical differences in sea surface temperature (SST) at 3 m, salinity (SSS), and anchovy density (number of fish/10^6 m^3) determined from each haul among years for the Predator Study, among cruises for the GLOBEC Study, and among years for Plume Study cruises in June and September because the values were not normally distributed. When significant differences were found, we used a Wilcoxon signed-rank test to detect differences among cruises/years, adopting a Bonferroni adjusted significance level to account for the number of comparisons being made.

We used simple linear regression to identify the relationship between anchovy densities and distance from shore for Predator Study catches after accounting for the effect of year with an extra-sum-of-squares F-test. We used multiple linear regression models to explore any relationship between observed anchovy densities and physical and biological oceanography during Plume Study cruises (1998–2006) in June and September, modeling *in situ* surface (3 m) SST, SSS, sea surface density (SSD), chlorophyll *a*, and station depth as independent predictor variables and anchovy density as the dependent response. Anchovy densities were $\ln(x+1)$ transformed before analysis because of the high proportion of hauls containing zero catch. We tested residuals for normality using the χ^2 goodness-of-fit statistic and compared models with an extra-sum-of-squares F-test.

We conducted correlation analyses between age-1 anchovy densities (that were measured from Predator Study catches April through June 1998–2006) and PDO and MEI values. We also conducted correlation analyses between age-1 anchovy densities and one-year lagged northern copepod biomass anomalies off Newport, Oregon, and one-year lagged timing of the spring transition. Advantages of lagged models are their predictive power and their ability to forecast fish densities one year into the future using current physical oceanographic data; these are highly desirable abilities in managing coastal pelagic species. The spring transition date was recorded as day of the year. Values for the northern copepod anomaly came from three "cold-water" copepod species, *Pseudocalanus mimus*, *Acartia longiremis,* and *Calanus marshallae*, identified and enumerated from biweekly sampling cruises off Newport, Oregon (Keister and Peterson 2003; Peterson and Schwing 2003). We considered a $p < 0.05$ to indicate a significant relationship for regression models and statistical correlation tests.

RESULTS

Trends in Abundance

Commercial landings and fishery-independent surveys showed strong evidence that anchovy abundance increased over the study period. Commercial catches of the northern subpopulation of northern anchovy in the Pacific Northwest increased from 68 mt in 2001 to 239

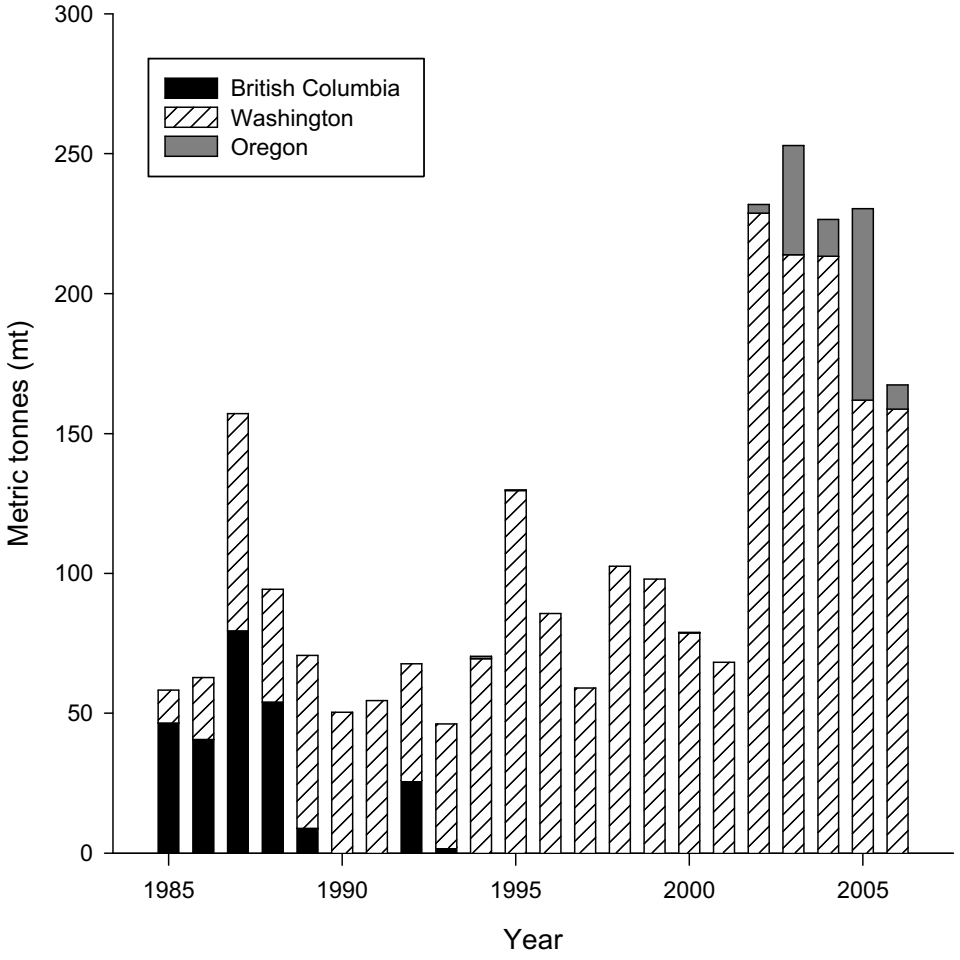

Figure 2. Annual commercial landings from 1985–2006 in mt of northern anchovy (*Engraulis mordax*) off Oregon, Washington, and British Columbia [data courtesy of B. Culver (WDFW), J. McCrae (ODFW), and T. Therriault (DFO)]. No metric for effort provided.

mt in 2002 (fig. 2). Anchovy landings were almost exclusively directed to a bait fishery centered off the Columbia River. Washington State recorded the highest catch numbers, with landings tripling between 2001 and 2002, but landings in Oregon also increased after 2001 (fig. 2). Anchovy have recently been observed to be relatively abundant in Puget Sound and north into the Juan de Fuca Strait, suggesting that interest in the fishery may increase with time (T. Therriault, DFO, pers. comm.).

Spatio-temporal Variance in Anchovy Abundance and Distribution

Fishery-independent sampling efforts show interannual variability in anchovy catch. Anchovy were landed as incidental bycatch in the Triennial Study beginning in 1977, although for the first two cruises, all catches occurred south of the Columbia River (fig. 3). Anchovy numbers increased during the ENSO event of 1983, and were encountered farther north than during any survey before or since. After 1986, northern anchovy were not encountered during Triennial Study surveys off the Pacific Northwest until 1998.

Anchovy distribution and abundance collected during the Plume Study had considerable inter-annual and seasonal variation. Anchovy landings during May (not shown) were patchy during all years except 2002, when we caught high densities of anchovy ($53{,}118/10^6$ m^3) off the mouth of the Columbia River. June Plume Study cruises sampled very few anchovy from 1998–2000 (fig. 4), with the exception of one huge haul (density = $12{,}127/10^6$ m^3) recorded off the Columbia River in 2000. The catch leveled off from 2001–02, with densities measuring 0–$55/10^6$ m^3 (fig. 4). However, beginning in June 2003, a coast-wide expansion of anchovy was observed. Anchovy were caught at 17 of 60 stations with densities >$3{,}000/10^6$ m^3 at four of those stations located off Cape Meares and the Columbia River (fig. 4). From June 2004 through 2005, anchovy were observed at 56 out of 91 stations from 44.5° to 48°N latitude, with the

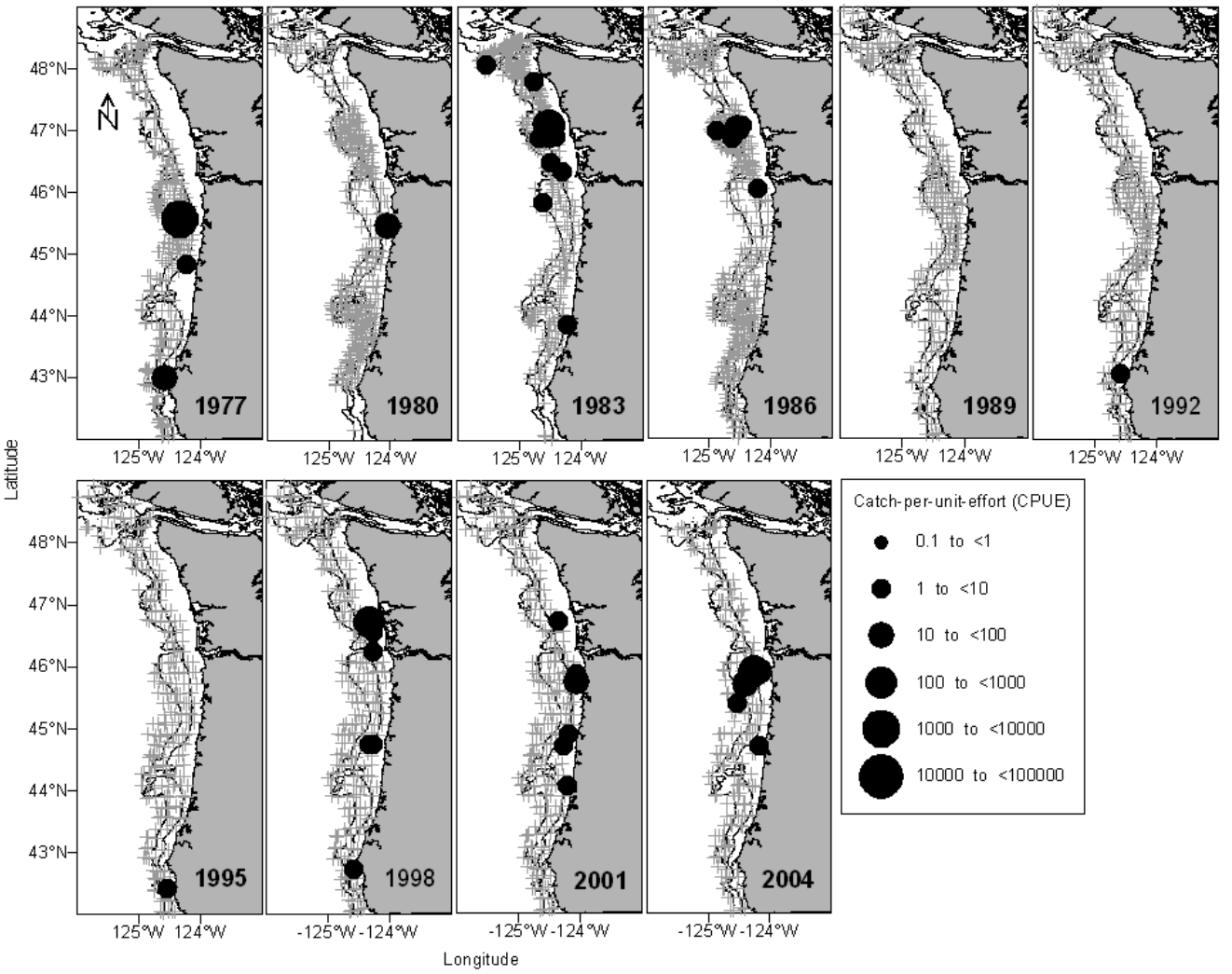

Figure 3. Catches of northern anchovy (*Engraulis mordax*) displayed as catch-per-unit effort (CPUE) from National Marine Fisheries Service (NMFS) Triennial Study cruises. All cruises occurred in June-September every three years from 1977–2004. Anchovy landed were incidental bycatch captured in the nets during deployment or retrieval of ground-fishing gear (bottom trawls). Stations fished where no anchovy were caught are denoted by a + symbol. Also shown are 100 and 200 m depth contours.

highest catches (22,913/10^6 m^3) found off the mouth of the Columbia River. In June 2006, anchovy numbers decreased (fig. 4), which coincided with increased southerly catches. For the first time during the Plume Study, the largest anchovy catches (106 and 180/10^6 m^3) occurred beyond the shelf break in deep water (>200 m), more than 50 km from the coast (fig. 4).

Distribution of anchovy during September Plume Study cruises did not always correspond well with Plume Study catch data during June of the same year. In September 1998, we caught higher densities of anchovy (0–61/10^6 m^3) than during the preceding June (0–35/10^6 m^3) (fig 5). However, in September 2000, anchovy were caught at record low densities (0–1/10^6 m^3). During September 2001, anchovy were mainly aggregated nearshore south of the Columbia River. We recorded small catches (1–15/10^6 m^3) south of the Columbia River in September 2002, at 18 of 65 stations along three transects (Cape Meares, Cascade Head, and Newport, Oregon). Higher densities of anchovy were caught (1–7,345/10^6 m^3) in September 2003, at 10 of 39 stations, with most occurring off Willapa Bay, Washington (fig. 5). In September 2004, we recorded anchovy at 33 of 47 stations along all eight transects sampled (1–21,400/10^6 m^3), indicating that the recruitment pulse observed in June 2004 persisted throughout the summer (fig. 5). Large anchovy densities were also recorded at 25 of 42 stations in September 2005 (1–12,809/10^6 m^3), although none occurred north of Grays Harbor, Washington. In September 2006, anchovy catch decreased, with densities ranging from 1–254/10^6 m^3 at 25 of the 55 stations fished (fig. 5).

GLOBEC Study distribution and abundance of anchovy off southern Oregon was patchy during all cruises

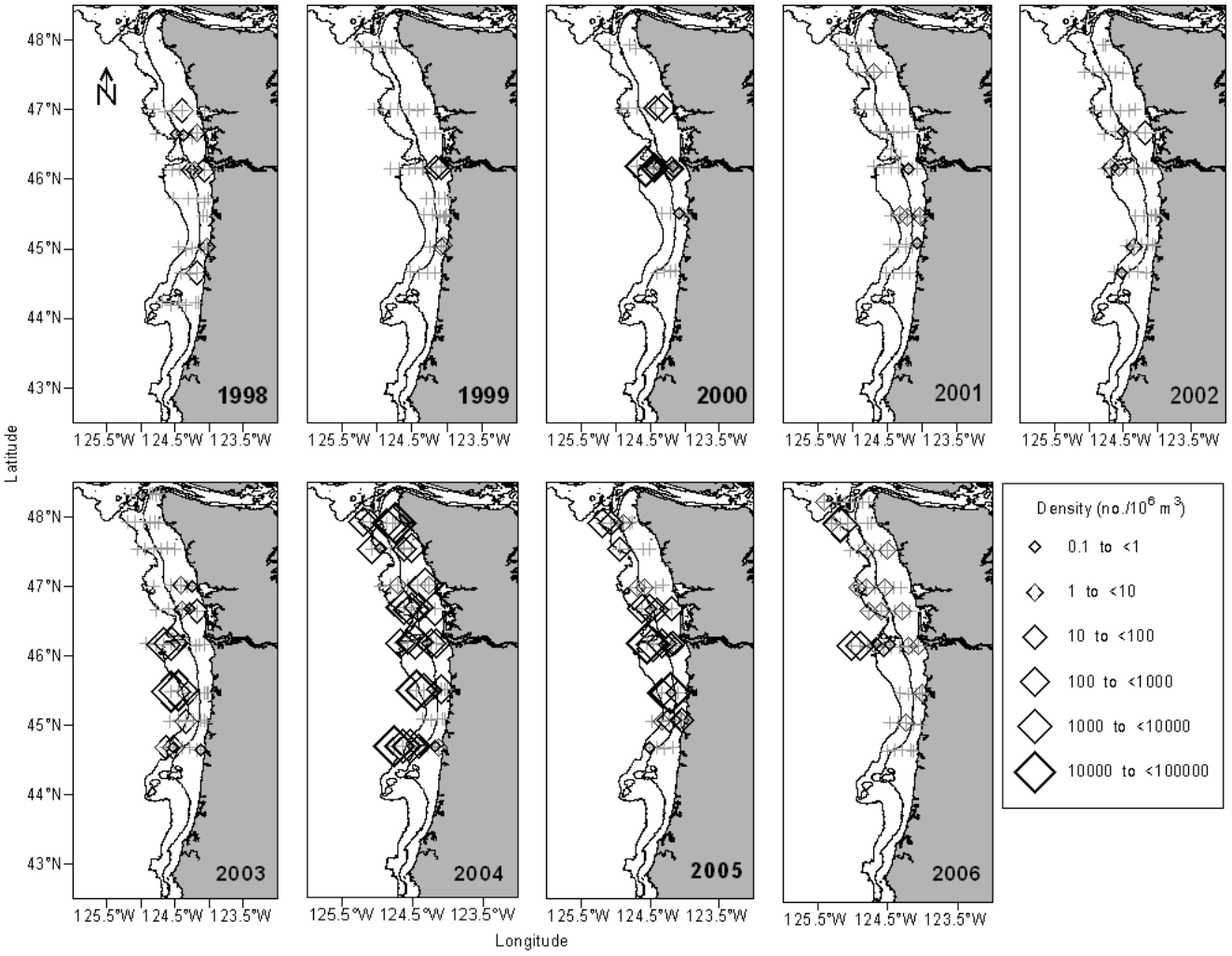

Figure 4. Distribution of northern anchovy (*Engraulis mordax*) density during Plume Study cruises (1998–2006) off Oregon and Washington in June standardized across hauls to number/10^6 m^3. The + signs show locations of surface trawls. Also shown are 100 and 200 m depth contours.

(fig. 6). No anchovy were captured in June 2000, but anchovy were caught at eight of 104 stations in June 2002 at densities orders of magnitude lower (0–15/10^6 m^3) than those in Plume Study catches at the mouth of the Columbia River during the same month (0–12,127/10^6 m^3) (fig. 4). In the GLOBEC Study, anchovy densities averaged 1/10^6 m^3 at 15 of 77 stations during August 2000, and ranged from 1–30/10^6 m^3 at 14 of 95 stations in August 2002 (fig. 6). We conducted an additional Plume Study cruise in August 2005 with transects sampled north of Newport, Oregon, to Grays Harbor, Washington. Large catches of anchovy were recorded, with densities (not shown) ranging from 0–4,546/10^6 m^3.

Predator Study anchovy densities from around the mouth of the Columbia River showed very large monthly and annual variability through spring and summer 1999–2006 (fig. 7). Large catches of anchovy were recorded in April 2003 (8,519/10^6 m^3). However, monthly averages from 1999–2006 were generally highest in May (2,458/10^6 m^3). Lowest anchovy densities were recorded in April and June 1999 and August 2001.

Anchovy densities were highest close to shore (fig. 8) during all Predator Study cruises, even after accounting for the effect of year (extra-sum-of-squares F-test, $F_{9,873} = 40.9$, $p < 0.001$). With the exception of 2003, highest anchovy catches were 0–10 km offshore, although anchovy were caught out to 60 km offshore every year (fig. 8). During 2001 and 2002, mean nearshore (<10 km) anchovy densities were three times greater than any offshore station (>10 km); in 2005 they were twice as large as any offshore station (>10 km).

Correlation of Abundance with Abiotic Factors

Northern anchovy distributions are likely strongly affected by abiotic factors such as sea surface temperature (3 m SST) and salinity (3 m SSS). Anchovy density var-

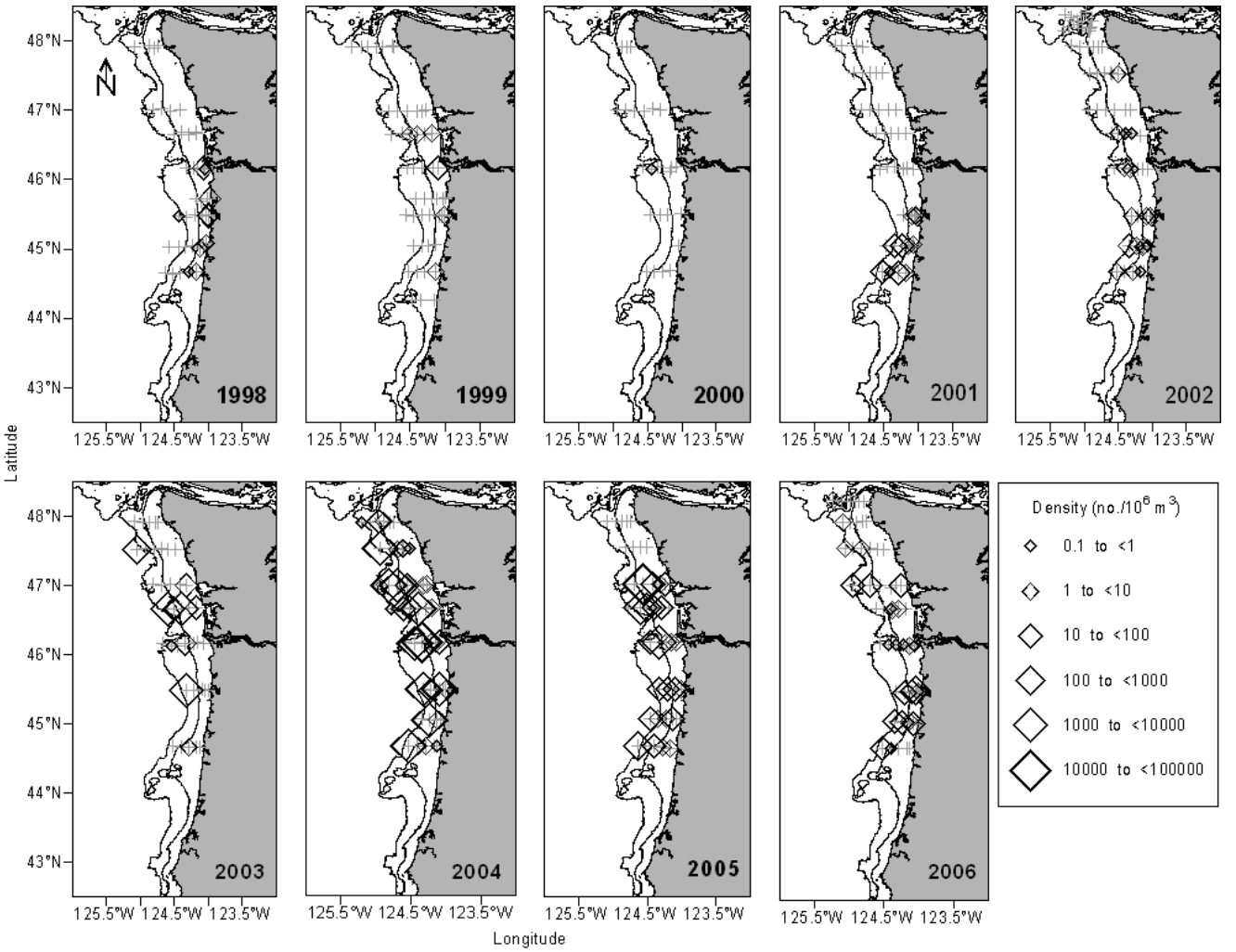

Figure 5. Distribution of northern anchovy (*Engraulis mordax*) density during Plume Study cruises (1998–2006) off Oregon and Washington in September standardized across hauls to number/10^6 m^3. The + signs show locations of surface trawls. Also shown are 100 and 200 m depth contours.

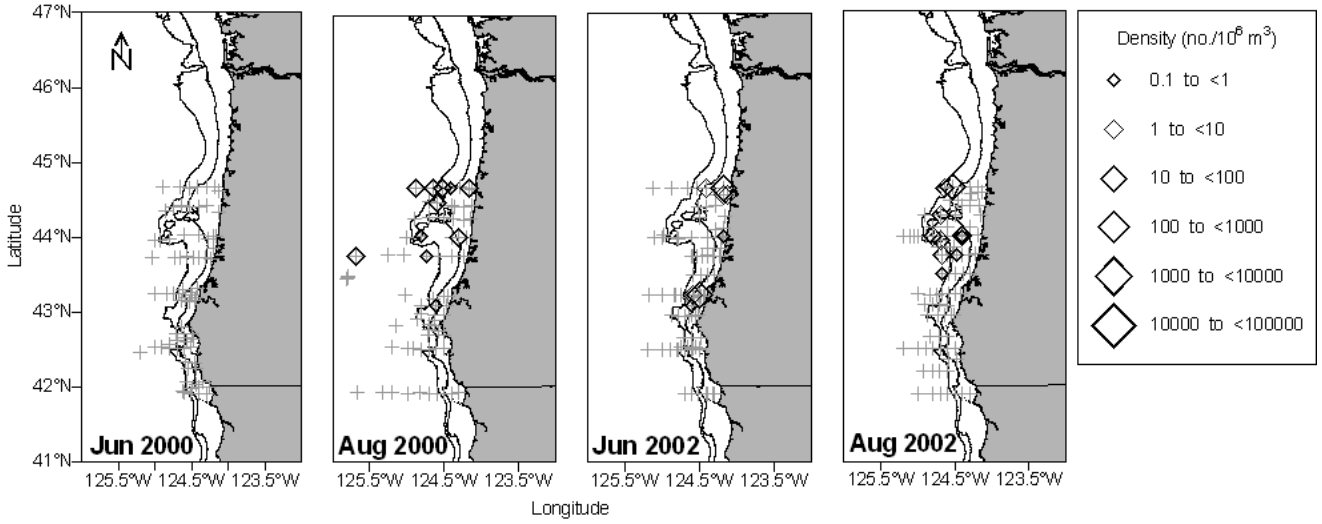

Figure 6. Northern anchovy (*Engraulis mordax*) density (standardized across hauls to number/10^6 m^3) for the 2000 and 2002 GLOBEC Study cruises off southern Oregon and northern California. The + signs show locations of surface trawls. Also shown are the 100 and 200 m depth contours.

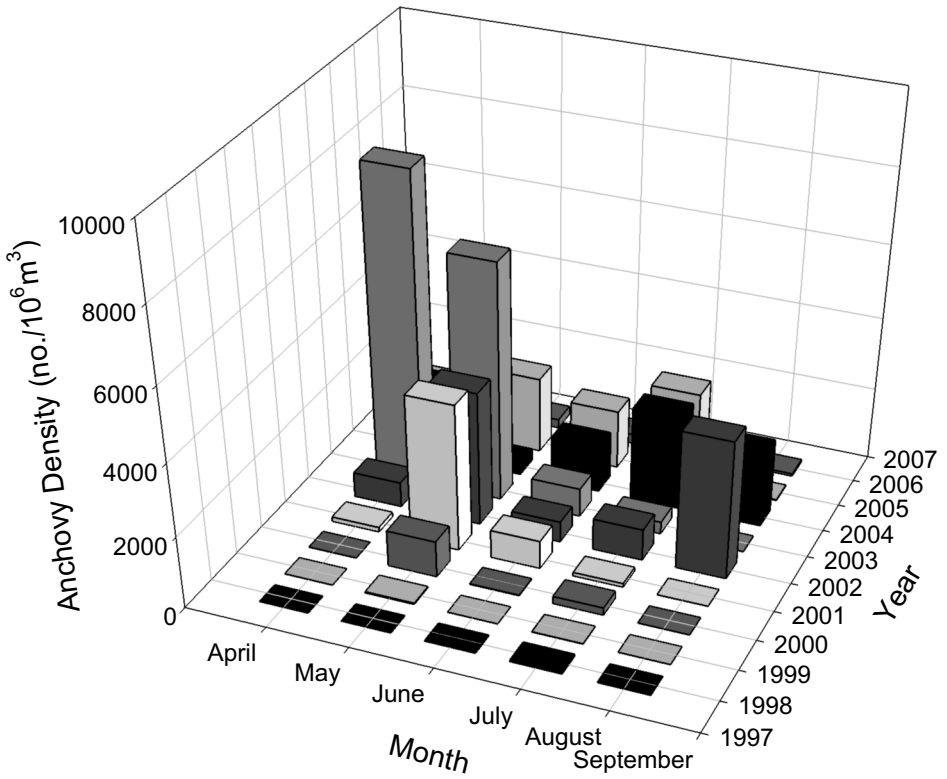

Figure 7. Average monthly densities (standardized across hauls to number/10^6 m^3) of northern anchovy (*Engraulis mordax*) captured from 1998–2006 during Predator Study cruises. Sampling occurred from April through September at stations associated with the Columbia River plume in 1998, and along two transects north and south of the Columbia River (1999–2006).

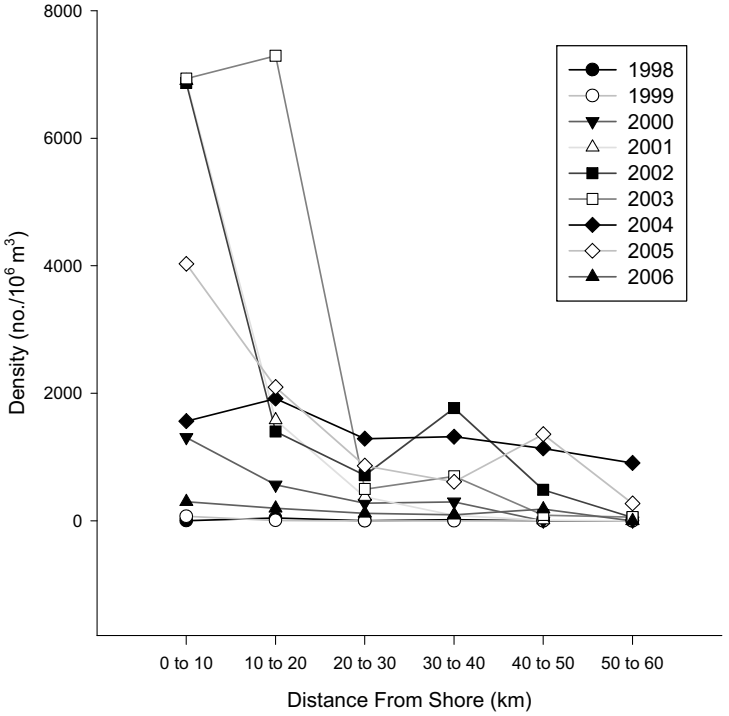

Figure 8. Average annual density (standardized to number/10^6 m^3) of northern anchovy (*Engraulis mordax*) at 0–60 km from shore, 1998–2006. Predator Study cruises that sampled from April through September at stations associated with the Columbia River plume in 1998, and along two transects north and south of the Columbia River (1999–2006).

TABLE 2

Mean ± one standard deviation surrounding the mean (SD) from *n* observations of sea surface (3 m) temperature (°C), salinity (psu), and northern anchovy (*Engraulis mordax*) density (number/10^6 m^3) measurements made during NMFS Predator Study cruises (1998–2006) in the northern California Current. Values of temperature, salinity, and anchovy density that do not share a common superscript have significantly different medians ($p < 0.001$, Kruskal-Wallis rank sum test and $p < 0.006$, Wilcoxon signed-rank test).

		Temperature (°C)		Salinity (psu)		Anchovy (no./10^6 m^3)	
Year	*n*	Mean	±SD	Mean	±SD	Mean	±SD
1998	46	14.3^{a}	1.2	28.9^{ab}	3.5	23.8^{e}	115.0
1999	109	11.8^{d}	1.2	29.1^{b}	2.8	11.9^{e}	102.0
2000	96	12.7^{c}	1.3	29.3^{a}	3.0	458.0^{bd}	2293.0
2001	106	12.5^{c}	1.2	30.8^{a}	1.9	1668.0^{b}	12069.0
2002	110	12.8^{c}	2.2	29.4^{b}	2.8	1831.0^{ad}	9861.0
2003	113	13.0^{c}	1.6	29.7^{b}	2.2	3327.0^{ac}	12646.0
2004	105	14.1^{b}	1.5	29.4^{b}	2.6	1458.0^{bc}	3310.0
2005	118	13.9^{b}	1.6	29.2^{b}	2.7	1591.0^{b}	3501.0
2006	80	12.8^{c}	1.5	31.0^{a}	1.7	157.0^{d}	385.0

TABLE 3

Mean ± one standard deviation surrounding the mean (SD) from *n* observations of sea surface (3 m) temperature (°C), salinity (psu), and northern anchovy (*Engraulis mordax*) density (number/10^6 m^3) measurements made during NMFS GLOBEC Study cruises (2000, 2002) in the northern California Current. Values of temperature, salinity, and anchovy density that do not share a common superscript have significantly different medians ($p < 0.001$, Kruskal-Wallis rank sum test and $p < 0.006$, Wilcoxon signed-rank test).

		Temperature (°C)		Salinity (psu)		Anchovy (no./10^6 m^3)	
Year	*n*	Mean	±SD	Mean	±SD	Mean	±SD
June 2000	91	12.0^{a}	1.3	32.0^{d}	0.6	0.0^{b}	0.0
Aug 2000	77	12.2^{a}	2.4	33.0^{b}	0.5	0.6^{a}	1.6
June 2002	104	11.1^{b}	1.6	32.3^{c}	0.9	0.3^{ab}	1.8
Aug 2002	95	10.3^{c}	1.3	33.3^{a}	0.5	0.8^{a}	3.3

TABLE 4

Mean ± one standard deviation surrounding the mean (SD) from *n* observations of sea surface (3 m) temperature (°C), salinity (psu), and northern anchovy (*Engraulis mordax*) density (number/10^6 m^3) measurements made during NMFS Plume Study cruises (1998–2006) in June in the northern California Current. Values of temperature, salinity, and anchovy density that do not share a common superscript have significantly different medians ($p < 0.001$, Kruskal-Wallis rank sum test and $p < 0.006$, Wilcoxon signed-rank test).

		Temperature (°C)		Salinity (psu)		Anchovy (no./10^6 m^3)	
Year	*n*	Mean	±SD	Mean	±SD	Mean	±SD
1998	39	12.4^{ef}	1.4	31.4^{ac}	1.6	2.6^{def}	7.9
1999	47	13.9^{b}	1.0	28.1^{f}	3.1	1.1^{f}	5.4
2000	48	12.4^{ef}	1.2	29.7^{ef}	2.3	265.0^{bcd}	1749.0
2001	49	13.2^{ce}	1.1	31.7^{a}	1.0	0.3^{ef}	1.2
2002	46	14.0^{b}	1.5	30.3^{cde}	2.4	1.3^{cf}	8.0
2003	60	12.3^{df}	1.7	31.7^{ab}	0.9	608.0^{def}	2652.0
2004	50	14.4^{ab}	1.9	30.8^{cd}	1.9	1603.0^{a}	3582.0
2005	41	14.9^{a}	1.0	30.1^{de}	1.4	952.0^{ab}	3899.0
2006	59	13.1^{bcd}	2.1	31.2^{bcd}	1.6	57.8^{de}	399.0

ied considerably among years during the Predator Study (tab. 2), among cruises during the GLOBEC Study (tab. 3), and among years during June and September Plume Study cruises (tabs. 4–5). SST differed significantly among years and cruises for all studies (Kruskal-Wallis; $p < 0.001$); among Predator and Plume Studies, SST was highest in 1998, 2004, and 2005 and lowest in 1999 (Wilcoxon, $p < 0.006$), with the exception of the June Plume Study (tab. 4) and the September 2005 Plume Study (tab. 5), when SST fell by an average of 3°C following delayed coastal upwelling (Schwing et al. 2006). Low SST values were recorded during Predator and September Plume Study cruises in 1999, and corresponded to La Niña conditions (tabs. 2, 4–5) (Brodeur et al. 2005).

TABLE 5

Mean ± one standard deviation surrounding the mean (SD) from *n* observations of sea surface (3 m) temperature (°C), salinity (psu), and northern anchovy (*Engraulis mordax*) density (number/10^6 m^3) measurements made during NMFS Plume Study cruises (1998–2006) in September in the northern California Current. Values of temperature, salinity, and anchovy density that do not share a common superscript have significantly different medians ($p < 0.001$, Kruskal-Wallis rank sum test and $p < 0.006$, Wilcoxon signed-rank test).

		Temperature (°C)		Salinity (psu)		Anchovy (no./10^6 m^3)	
Year	*n*	Mean	±SD	Mean	±SD	Mean	±SD
1998	46	13.2^{bd}	1.2	31.8^{cd}	0.9	3.9^{bc}	11.4
1999	49	11.7^{f}	1.4	32.3^{ac}	0.6	1.7^{c}	8.9
2000	24	13.6^{abc}	2.1	30.6^{ef}	2.3	0.0^{bc}	0.2
2001	46	12.6^{bcd}	1.1	32.0^{acde}	0.9	4.6^{bc}	14.7
2002	65	12.1^{bd}	1.6	32.4^{ab}	0.3	0.9^{c}	2.4
2003	39	13.0^{bd}	1.5	31.7^{cde}	1.1	403.0^{abc}	1463.0
2004	47	14.5^{a}	1.4	31.0^{f}	1.7	1278.0^{a}	3705.0
2005	42	11.9^{cef}	1.6	32.4^{a}	0.8	472.0^{a}	2096.0
2006	55	12.6^{de}	1.1	31.7^{bef}	1.4	10.9^{b}	35.8

TABLE 6

Regression coefficients, standard errors, and *p*-values (statistically significant main effects in bold) from the multiple regression models applied to ln(χ+1) northern anchovy (*Engraulis mordax*) density (number/10^6 m^3) during Plume Study cruises (1998–2006) in June and September.

Variable	Plume	June	*n* = 265	Plume	September	*n* = 413
	Coefficient	SE	*p*	Coefficient	SE	*p*
Intercept	–6.068	3.361	0.072	–0.284	7.379	0.969
Depth	0.000	0.001	0.919	0.000	0.001	0.823
Temperature	0.392	0.309	0.205	–0.417	0.728	0.567
Salinity	0.208	1.227	0.865	–3.081	2.960	0.299
Density	–0.201	1.575	0.898	–3.823	3.819	0.317
Chl-	0.034	0.023	0.138	0.034	0.021	0.113

Variable	Plume	June	*n* = 265	Plume	September	*n* = 413
	Coefficient	SE	*p*	Coefficient	SE	*p*
Intercept	**–6.489**	**2.269**	**0.004**	**–7.062**	**3.472**	**0.043**
Depth	0.000	0.001	0.918	0.000	0.001	0.828
Temperature	**0.442**	**0.078**	**<0.001**	**0.336**	**0.082**	**<0.001**
Density	0.066	0.067	0.324	0.150	0.112	0.180
Chl-	0.034	0.023	0.140	0.033	0.021	0.128

Variable	Plume	June	*n* = 265	Plume	September	*n* = 413
	Coefficient	SE	*p*	Coefficient	SE	*p*
Intercept	**–4.434**	**0.899**	**<0.001**	**–2.503**	**0.731**	**<0.001**
Depth	0.000	0.001	0.751	0.001	0.001	0.680
Temperature	**0.400**	**0.035**	**<0.001**	**0.259**	**0.059**	**<0.001**
Chl-	0.033	0.023	0.149	0.030	0.021	0.154

Variable	Plume	June	*n* = 265	Plume	September	*n* = 413
	Coefficient	SE	*p*	Coefficient	SE	*p*
Intercept	**–4.463**	**0.894**	**<0.001**	**–2.531**	**0.727**	**<0.001**
Temperature	**0.405**	**0.064**	**<0.001**	**0.266**	**0.057**	**<0.001**
Chl-	0.032	0.022	0.160	0.028	0.021	0.172

Variable	Plume	June	*n* = 265	Plume	September	*n* = 413
	Coefficient	SE	*p*	Coefficient	SE	*p*
Intercept	**–3.871**	**0.792**	**<0.001**	**–2.443**	**0.725**	**<0.001**
Temperature	**0.369**	**0.059**	**<0.001**	**0.269**	**0.057**	**<0.001**

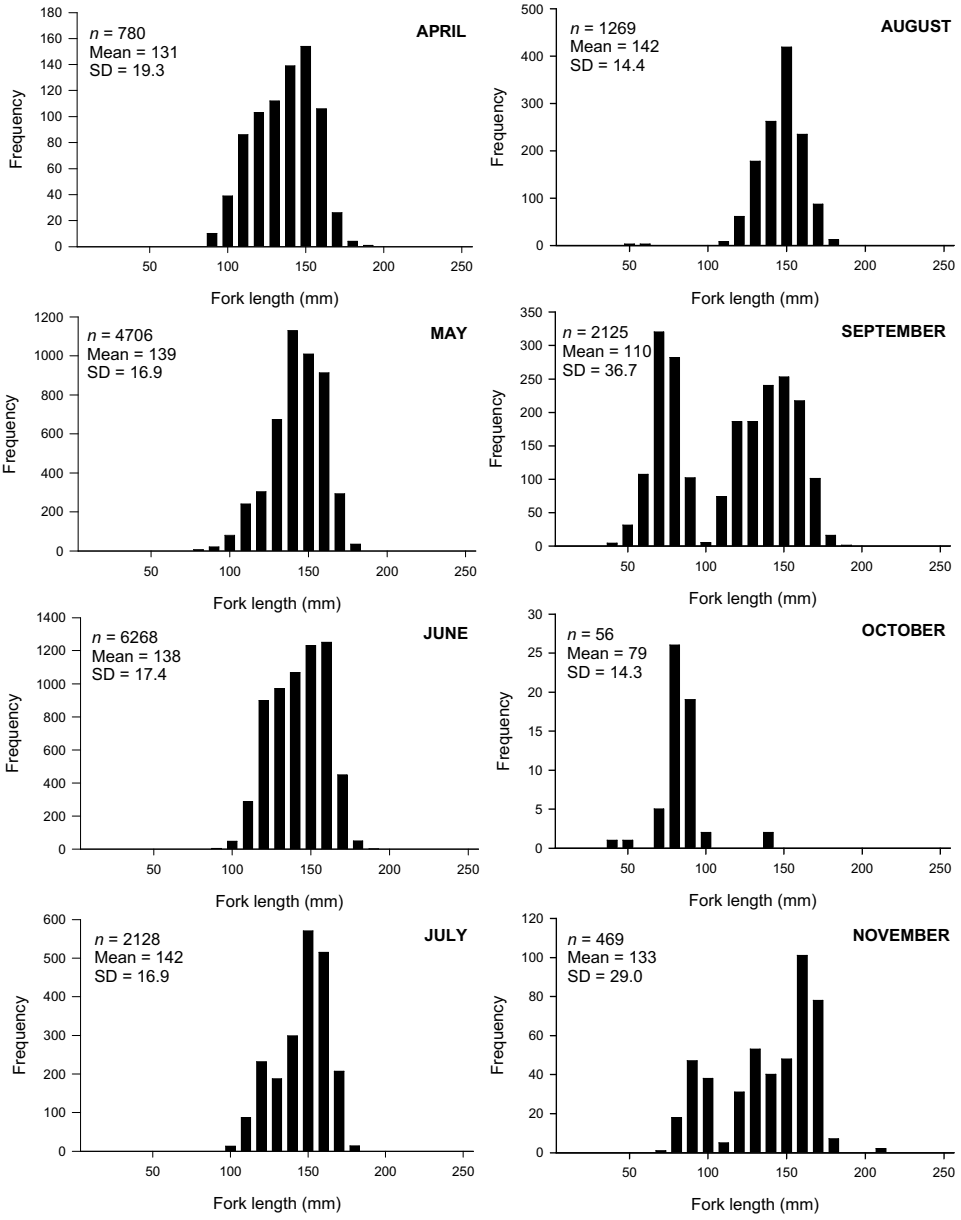

Figure 9. Monthly length-frequency histograms showing pooled northern anchovy (*Engraulis mordax*) fork lengths (mm) measured from 1998–2006 during National Marine Fisheries Service Predator and Plume Study cruises. For each month, we recorded the total number (*n*) of measurements, mean, and one standard deviation surrounding the mean (SD). Note the appearance of a second cohort from August through November, indicating recruitment of summer-spawned juveniles.

SSS was significantly different among all years and cruises for Predator, GLOBEC, and Plume Studies (Kruskal-Wallis, $p < 0.001$) however, seasonal variations were also detected. SSS values were highest in September during all Plume Study cruises (tab. 5). Differences in SSS were probably related to Columbia River flows and upwelling intensity. For example, mean SSS values were greatest during all GLOBEC Study cruises (tab. 3), which occurred at the southern end of the Columbia River plume front in a region of stronger coastal upwelling. We observed higher SSS values (Wilcoxon, $p < 0.006$) in Predator and Plume Studies in 2001 and 2006 compared to all other years (tabs. 2, 4–5).

Anchovy densities (number/10^6 m^3) varied significantly among all years/cruises for Predator, GLOBEC, and Plume Studies (Kruskal-Wallis, $p < 0.001$). We recorded zero to small catch densities in 1998 and 1999 during Predator and Plume Studies (tabs. 2, 4–5). From 2002–04, anchovy densities increased significantly (Wilcoxon, $p < 0.006$), although the year of peak abundance depended on the study. Predator Study anchovy densities peaked in 2003; Plume Study anchovy densities

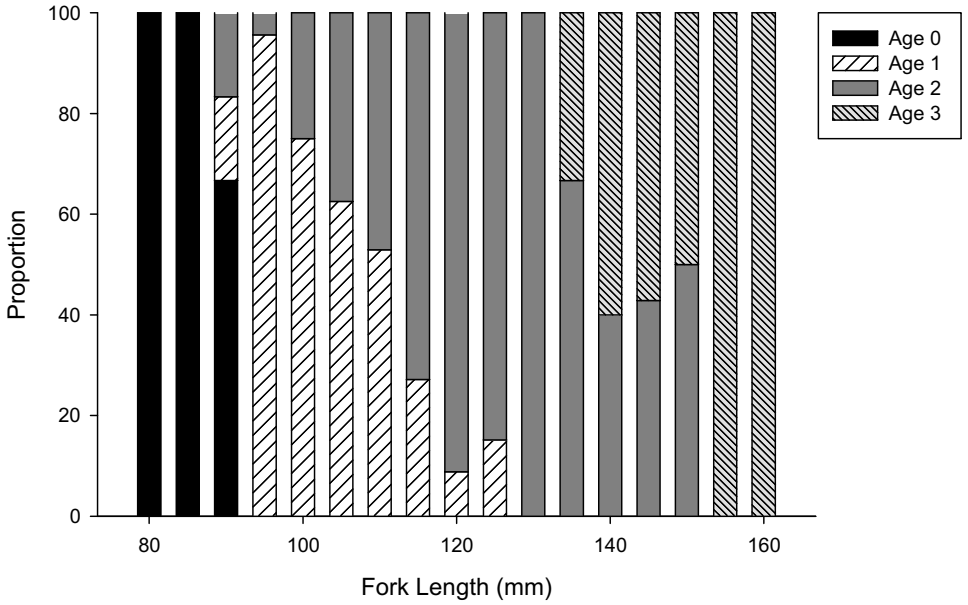

Figure 10. A length-frequency age-overlay histogram developed by aging 295 pairs of northern anchovy (*Engraulis mordax*) saggital otoliths, sampled from fish collected during April-August 2005 Predator Study cruises. Age was determined as the median of three reads performed on different days.

in June and September peaked in 2004. Following 2004, anchovy catch densities significantly decreased (Wilcoxon, $p < 0.006$) throughout Predator and Plume Study cruises (tabs. 2, 4–5), a trend that continued through 2006.

When modeled independently, SST was the single most consistent environmental parameter explaining anchovy abundance during Plume Study cruises (ANOVA, $p < 0.001$) in June and September. The relationship between catch and SST was positive for all cruises (tab. 6). SST alone explained anchovy density during June (extra-sum-of-squares *F*-test, $F_{1,437} = 39.46$, $p < 0.001$) and September (extra-sum-of-squares *F*-test, $F_{1,411} = 22.57$, $p < 0.001$). Most anchovy were caught when the 3 m depth temperature was >12°C. All other variables were insignificant predictors of anchovy density across all Plume Study cruises (tab. 6).

Length and Age Frequencies

Length measurements of anchovy caught during the summertime 1998 and 2001 Triennial Studies ranged from 90–180 mm FL, and during the April-November Plume, GLOBEC, and Predator Studies lengths ranged from 30–265 mm FL, representing several age classes. We developed monthly histograms of size frequency for the Predator and Plume Study cruises because fork length information was logged more habitually (fig. 9). Analysis of length frequencies indicated that three size classes of anchovies were caught, with small fish noticeable in April (70–110 mm FL), and September (30–40 mm FL) through November (70–100 mm FL). While the large size classes (140–180 mm FL) were present each year, the smaller classes were not. The smaller anchovies seen in April appear to be sub-yearlings spawned the previous summer. The smallest anchovies seen in September through November (fig. 9) were young-of-the-year (YOY) spawned off Oregon and Washington during summer months.

Age analysis of 295 anchovies captured from April through September during the nighttime Predator Study indicates that anchovy ranged from 0–3 years in age. We determined an average percent error of 0.06%, indicating extremely high reading precision, and created a length-frequency-by-age histogram (fig. 10).

A negative linear relationship was observed between timing of the spring transition and age-1 anchovy survival, and positive relationships between PDO, MEI, and age-1 survival (fig. 11), although none of the relationships were significant (GLM, $p > 0.05$). However, anomalies of northern copepod biomass showed a significant positive relationship to age-1 anchovy survival (fig. 11), accounting for 62% of the variation associated with the data (GLM, $p = 0.01$).

DISCUSSION

The large inter-annual variability in anchovy densities (number/10^6 m^3) off Oregon and Washington appears to be driven by SST and strong year-class strength due to environmental conditions affecting YOY. From 1998 to 2006, anchovy abundance in the CCLME showed very high temporal variability by year. Anchovy densities corresponded with fluctuations in the localized physical conditions off Oregon and Washington, namely

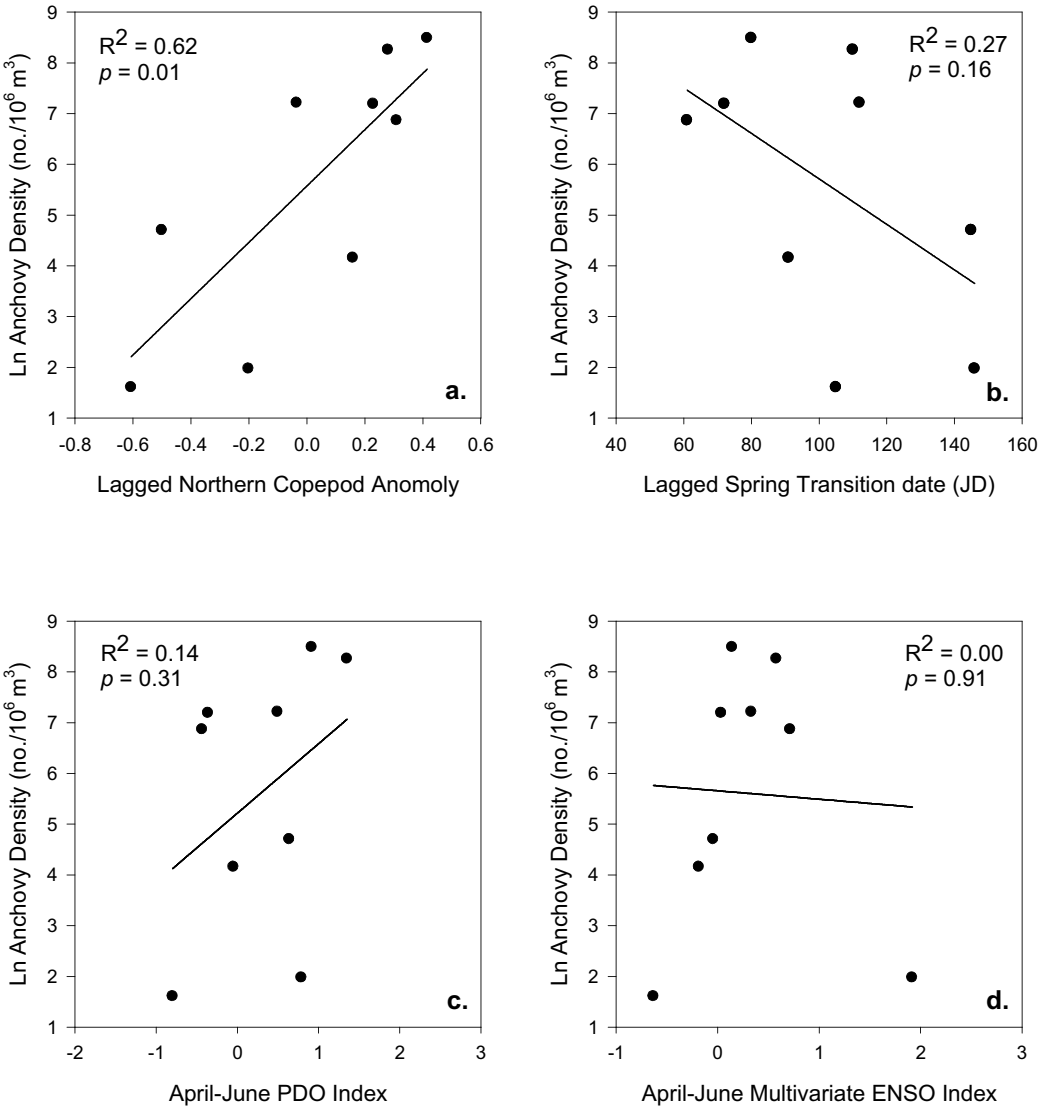

Figure 11. Correlation between log-transformed age-1 northern anchovy (*Engraulis mordax*) density (standardized to number/10^6 m^3) captured during Predator Study cruises in April-June (1998–2006) and (a) value of the one-year lagged northern copepod anomaly, (b) day of the year of the spring transition, (c) mean value of the April-June Pacific Decadal Oscillation (PDO) Index, and (d) mean value of the April-June Multivariate El Niño Southern Oscillation Index (MEI). *R*-squared values and corresponding *p*-values presented at a significance level <0.05.

SST. Warm SSTs were recorded in 1998, 2004, and 2005, and cool SSTs were recorded in 1999–2003 and in 2006. Low anchovy densities were recorded in 1998–2001 and 2005–06. High anchovy densities were recorded in 2002–04.

A shift in northeastern Pacific environmental conditions began in 1999 (Peterson and Schwing 2003), and is reflected in large-scale forcing indices of the North Pacific Ocean, including the PDO and MEI. From 1991 to 1998, PDO and MEI values were primarily positive. However, beginning in late-1998, they became negative, turning positive again in the middle of 2002 and staying positive through 2006. During the 1990s, a very warm period of the PDO was punctuated by ENSO events, and no forage fishes were captured in high abundances off Oregon and Washington (Emmett and Brodeur 2000) until Pacific sardine numbers increased dramatically in the Pacific Northwest accompanying the 1992–93 ENSO (Emmett et al. 2005). Warm ocean conditions persisted through 1997 and 1998, but from 1999 to 2002 the ocean was cold. Northern anchovy eggs and larvae were the most abundant of 34 taxa collected during plankton sampling that occurred approximately every two weeks off the mouth of the Columbia River during spring and summer 1999–2004 (Parnel et al. 2008). In fact, anchovy were frequently captured near the mouth of the Columbia River, within the plume area, indicating some tolerance for fresh water.

Spawning studies of the northern subpopulation of northern anchovy (Richardson 1981; Emmett et al. 1997) indicate that prior to 1997, the spawning peak occurred in July. Recent evidence suggests that spawning can begin as early as May when anchovy congregate near the mouth of the Columbia River (Parnel et al. 2008). Determining the age of YOY anchovy captured during the September Plume Study by counting daily increments will contribute to our understanding of the relationship between hatch date and cohort strength (Takahashi and Watanabe 2004). It is possible that older anchovy females have the capacity to spawn earlier than younger fish, taking advantage of earlier spring transition dates. Studies have successfully linked variations in Pacific salmon marine survival with variations in the spring transition date with a lag of one year (Ryding and Skalski 1999; Logerwell et al. 2003).

Our multiple regression models for Plume Study cruises in June and September show a positive significant linear relationship between SST and anchovy density. However, our scope of inference is limited by the small amount of variability associated with measured SST values over the study period, as well as the significant relationship between age-1 survival and the lagged northern copepod biomass anomaly. There is substantial evidence that anchovy prefer cooler (10°–14°C) rather than warmer SSTs (Lluch-Belda et al. 1992; Schwartzlose et al. 1999; McFarlane and Beamish 2001; Rodriguez-Sanchez et al. 2002; Chavez et al. 2003; Van der Lingen et al. 2006). It is possible that all nearshore habitats we sampled were within the SST tolerances of northern anchovy, thereby reducing our ability to distinguish among SSTs that significantly affect anchovy density. What is more likely is that in situ SST did not effectively predict anchovy density so much as provide insight into YOY survival, so that our catch numbers (number/10^6 m^3) were more a reflection of ocean conditions the year before. This is a common result of gear selectivity, whereby mesh size selects for age-1+ fish. The year class strength of many fish populations, including anchovy, is determined in the first year of life (Bradford and Cabana 1997). Because the northern anchovy is short-lived, its abundance depends on recruitment success from year to year. Peaks in abundance (2003, 2004) were more due to successful recruitment, coupled with cool SSTs, early spring transitions, high primary productivity, and abundant northern zooplankton leading up to 2004, than to in situ warm SSTs recorded in that year. The Predator Study peak in 2003 was attributed to high densities (8,519/10^6 m^3) of subyearling anchovy caught during April, suggesting high over-wintering survival of recruits. This could be related to an intrusion of cold, low oxygen, subarctic water in 2002 (Wheeler et al. 2003).

Northern anchovy are part of a guild of planktivorous coastal pelagic species, whose prey includes phytoplankton and zooplankton (Miller and Brodeur 2007). Northern zooplankton species, namely cold-water boreal copepods, exhibit conservative life-history strategies allowing them to accumulate higher concentrations of poly-unsaturated fatty acids compared to southern, warm-water copepods (Davis and Olla 1992). Poly-unsaturated fatty acids include essential fatty acids that can only be obtained through diet, and greatly influence larval growth rate and survival (Watanabe 1993; Budge et al. 2006). The relationship between age-1 northern anchovy and the lagged northern copepod biomass anomaly must be recognized as an important measurable biological indicator of ocean productivity. The abundance of cold-water copepods may, in fact, be determining anchovy year-class strength. However, it should also be considered that the differences in the copepod community may be due to advection, and that unfavorable advective currents may also carry anchovy from favorable recruitment. Further monitoring will provide the data needed to safely and effectively manage coastal pelagic species in the northeastern Pacific Ocean.

Conclusions

Anchovy continues to be a dominant pelagic forage fish in the CCLME, and is increasingly caught by commercial fishermen whose primary interest is in its value as bait. The coexistence of northern anchovy and Pacific sardine in the CCLME over the past decade (Emmett et al. 2005) appears contradictory to theories about regime shifts for these two species and suggests that plankton is abundant and available enough to support multiple plankton-feeding pelagic schooling fishes. However, there may be intrinsic properties associated with the available plankton community that may lead to differences in energetic availability, which could, in turn, affect growth and survival. Our data suggest that proximity to shore, SST, and timing of the spring transition are important predictors of anchovy density, and fluctuations in the physical oceanographic parameters may have contributed to the decline observed in anchovy density during 2005 and 2006. Under certain conditions, such as delayed coastal upwelling (Schwing et al. 2006), the zooplankton community is influenced by decreased productivity and bottom-up effects, which in turn influences anchovy recruitment. The high 2006 northern copepod index predicts a successful 2007 age-1 anchovy year-class. However, continued observations and studies will be necessary to confirm this.

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IMPACTS OF INTERANNUAL ENVIRONMENTAL VARIATION ON THE SHRIMP FISHERY OFF THE GULF OF CALIFORNIA

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ABSTRACT

This work presents an exploratory analysis of the potential relationship between offshore shrimp catches and environmental factors at the Gulf of California, using shrimp harvest information from Guaymas, Sonora, and Mazatlán, Sinaloa, México. Multiple correlation analysis was used to examine the relationships between landings time series and environmental variables, including average rainfall, fluvial discharge, the Pacific Decadal Oscillation (PDO) and the El Niño Multivariate (MEI) Indices. Environmental index series were split for January through June (cold season) and July through December (warm season), since shrimp populations show two reproduction peaks throughout the year. These two spawning seasons give rise to two cohorts: the cold-season (April–June) and the warm-season (October–November), the former sustaining the fishery during the open season (September–March) and yielding 90% of total catch between September and October. Our findings indicate that the mean PDO index for the cold season accounted for the highest percentage of catch variation, suggesting that conditions during the cold season (January–June) may determine recruiting in the April–June cohort. This information may be used to derive catch forecasts several months in advance.

INTRODUCTION

The offshore shrimp fishery in the Gulf of California produces over 70% of the total shrimp harvested along the Mexican Pacific coast (Sierra et al. 2000); Guaymas, Sonora and Mazatlán, Sinaloa, are the two major fishing ports (fig. 1). The fishery consists of an artisanal fleet which is made up of small pangas (outboard powered boats) in inshore lagoons and the adjacent coasts at less

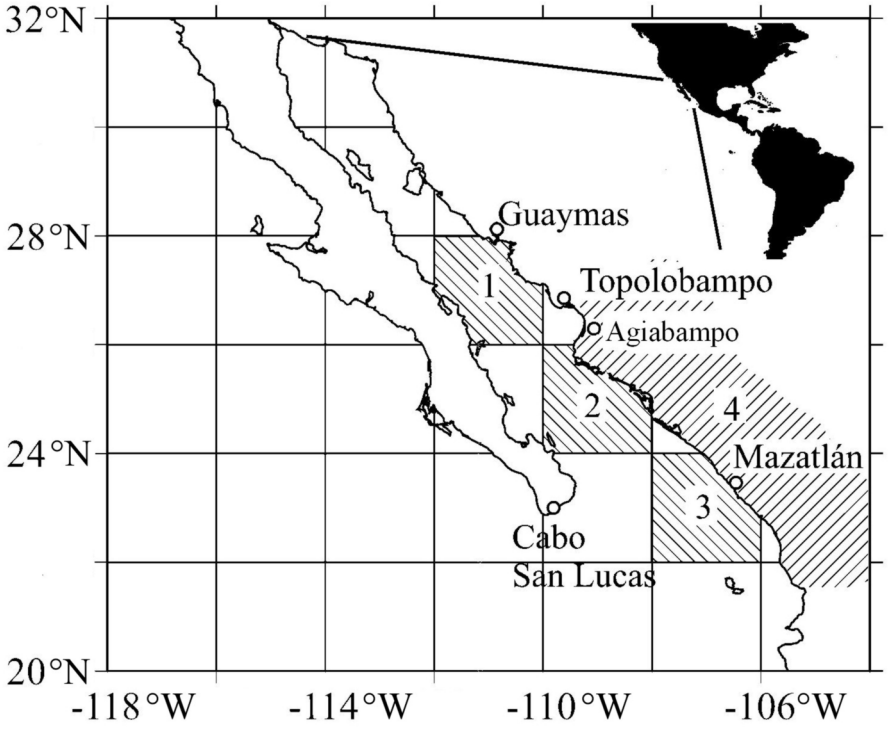

Figure 1. Location of quadrats for which sea surface temperatures (SST) were obtained (1, 2, and 3), and of the coastal meteorological stations and dams from which rainfall and incoming river flow data (4) were gathered.

than 5 fathoms deep, and an industrial fleet made up of shrimp trawlers fishing in offshore waters. The artisanal fleet is estimated at ca. 20,000, whereas the industrial fleet has more than 900 trawlers for Guaymas and Mazatlán (SEMARNAP, 2005). The industrial fleet has been operating since the 1970s under adverse economic conditions derived from overcapitalization (Meltzer and Chang 2006). This has resulted in low annual per-vessel catch yields, declining from some 24 tons during the 1960s to less than 10 tons, on average, over the past 15 years. The fishing season for the offshore fishery usually starts in mid-September and, although it may last six months, is more intense during the first two months when nearly 90% of total catch is harvested. These low yields make the industrial fleet particularly susceptible to natural fluctuations in shrimp abundance, with years of profits alternating with years of losses, so that a forecast tool allowing shrimp fishing operations to plan ahead of the fishing season would be useful.

It has long been suggested that the variability of penaeid shrimp abundance is related to the physical environment (Castro-Aguirre 1976; Vance et al. 1985; Catchpole and Auliciems 1999; Galindo-Bect et al. 2000; Lopez-Martinez et al. 2002; Lee 2004; Henderson et al. 2006). These fluctuations are identified through the variability of environmental factors such as temperature, rainfall, and fluvial discharge, which in turn are related to large-scale changes associated with atmospheric and oceanic circulation dynamics. Similar analyses have been conducted by Catchpole and Auliciems (1999), who found a positive correlation between the Southern Oscillation Index (SOI) and shrimp catch in northern Australia, which was related to rainfall seasonality. Norton and Mason (2005) analyzed the variability of fish and shellfish catches on the California coast along with information on environmental factors, and identified two variability patterns at a climatic scale that were related to the tropical and northern Pacific Ocean, and detected changes in catch composition and volume.

The resilience of shrimp populations derives from their short life cycle, which results in two shrimp cohorts per year. Brown shrimp (*Farfantepenaeus californiensis*) have been found to have two periods of major reproductive activity (Romero-Sedano et al. 2004), the first during June and July and the second between October and November. These may fluctuate according to seasonal variations in temperature (Leal-Gaxiola et al. 2001). Blue shrimp (*Litopenaeus stylirostris*) have also been found to have two reproduction peaks, the first from April to June, giving rise to the spring cohort, and the second from October to January, producing the fall cohort (López-Martínez et al. 2002). The timing of cohorts suggests that it is the spring cohort that supports the fishery which starts in September. White shrimp (*Litopenaeus vannamei*) have been documented to spawn along a prolonged period, May to September, but more intensely during the first and the last months (Sepúlveda 1991). Other aspects of shrimp biology and fisheries on the Pacific coast of México have been described by Magallón (1987), Sepúlveda (1981, 1991, and 1999), and others.

In this study we examine the feasibility of using local and large-scale environmental indices as forecasting tools for relative shrimp abundance. Since landings (and hence relative abundance) have been suggested to depend largely on recruitment during the cold part of the year prior to the fishing season, it is assumed that the environmental factors occurring during April through June may have a key influence on the next fishing season.

MATERIAL AND METHODS

Two sets of shrimp landings data from Guaymas, Sonora and Mazatlán, Sinaloa from Sierra et al. (2000) were analyzed. Guaymas data include catch time series for blue shrimp between 1985 and 1999, and both catch and CPUE (catch per unit of effort) for brown shrimp between 1975 and 1999; Mazatlán data include catch time series for blue, brown, and white shrimp between 1983 and 1999. Landings are from the offshore fishing season ranging from September to March of the following year, commonly beginning the second half of September. Also included are landings from the artisanal fishery (caught during August to February), except for those of brown shrimp at Guaymas (which are only from the industrial fleet) including CPUE information. Data are shown in Table 1.

Environmental information corresponds to two different geographic scales: regional data, including rainfall (P) and fluvial discharge (F); and large-scale indices, such as the Pacific Decadal Oscillation index (PDO), which accounts for the variability in the northern Pacific Ocean, and the El Niño Multivariate Index (MEI), which represents the variability in the tropical Pacific Ocean. Additionally, sea surface temperature (SST) and rainfall data were used to derive mean climate estimates of the seasonal variation. Table 2 includes a brief description of the type of information used and the respective source. SST data were obtained from the U.S. National Climatic Data Center (NCDC) database, whereas rainfall and fluvial discharge data were obtained from Brito-Castillo (2003) for coastal basins in Sonora and Sinaloa, as shown in Figure 1. Time series of environmental variables were averaged for two periods, one corresponding to the cold season, January to June, and the other corresponding to the warm season, July to December.

A first analysis, aimed at identifying the best indices for the purpose of forecasting, was performed by means of multiple linear correlations using each of the landings series (C) as the independent variables, seasonal averages

TABLE 1
Shrimp catch (metric tons) landed at Guaymas, Sonora, and Mazatlán, Sinaloa, México.

	Mazatlán Catch (tons)			Guaymas Catch (tons)		CPUE (t/trip)
Season	Blue	White	Brown	Blue	Brown	Brown
1975–76					1713.8	0.591
1976–77					3550	1.046
1977–78					2970	0.716
1978–79					3140	1.233
1979–80					2210	1.008
1980–81					2910	1.168
1981–82					2400	1.018
1982–83					1280	0.517
1983–84	4470	3360	2110		2150	1.120
1984–85	4270	2930	2100		1450	0.867
1985–86	5240	2760	1650	2950	2210	1.140
1986–87	4160	1450	1940	3400	2910	1.457
1987–88	6380	1840	2360	2920	2000	1.014
1988–89	4410	1030	2230	1610	1920	1.095
1989–90	4640	1400	2360	1560	2090	1.470
1990–91	3330	760	1430	1320	1400	0.798
1991–92	2110	1530	2550	1250	1570	0.783
1992–93	4040	1310	1860	1060	2150	0.821
1993–94	3620	1980	2800	1790	2440	1.025
1994–95	4240	1860	2490	2110	2800	1.292
1995–96	4240	1310	2380	2540	3140	1.414
1996–97	5700	1100	1630	2070	2560	1.152
1997–98	5700	2780	2200	2790	3550	1.880
1998–99	3870	1140	2060	1460	1600	0.736
1999–2000	6000	900	2340	2150	2400	

TABLE 2
Summary of climatic variation indices and sources.

MEI - Multivariate El Niño index, Wolter and Timlin 1998. Obtained from EOF analysis of central Pacific SST monthly anomalies. http://www.cdc.noaa.gov/people/klaus.wolter/MEI/table.html (Access date; June 2005)
PDO - Pacific Oscillation Decadal index, Mantua et al. 1997. Obtained through EOF analysis of North Pacific SST monthly anomalies. http://jisao.washington.edu/pdo/PDO.latest (Access date; May 2005)
P - Regional monthly rainfall obtained from climatologic stations from Sonora and Sinaloa. Digitalized data from figures in Brito-Castillo 2003.
F - Regional monthly inflow volumes at dams (millions m^3) from Sonora and Sinaloa. Digitalized data from figures in Brito-Castillo 2003.
SST - Monthly average sea surface temperature data from Extended Reconstructed Sea Surface Temperature (ERSST), 2° x 2° quadrants centered at 23°N–107°W; 25°N–109°W and 27°N–111°W. http://lwf.ncdc.noaa.gov/oa/climate/research/sst/sst.html (Access date, January 2006)
Climatological monthly data of rainfall from http://www.inegi.gob.mx/est/contenidos/espanol/rutinas/ept.asp?t=mamb98&c=5843 (Access date, January 2006)

for the cold season (subscript c), and seasonal averages for the warm season (subscript w):

$$C = b_0 + b_1PDO_c + b_2PDO_w + b_3MEI_c + b_4MEI_w + b_5P_c + b_6P_w + b_7F_c + b_8F_w.$$

Later, the two variables with the largest effect on observed variability were identified as those variables with the highest absolute value of the weighted beta coefficient because this indicated the relative weight of the variable as a predictor.

Then, series were filtered to eliminate high-frequency variability and to facilitate the visualization of the major longer-term variation modes. For data filtering, we used Hamming 5-year windows (StatSoft 1999). Landings series were cross correlated with climatic variables, both raw and filtered, considering the seasonal averages corresponding to the warm (July–December) and cold (January–June) seasons separately. Results are shown in Table 3.

In a second analysis, multiple-linear correlation was again conducted using each of the smoothed landings series as dependent variables and the two smoothed identified environmental series as independent variables. The

TABLE 3
Correlation matrix between catch time series and climatic variables for northeastern México, upper portion = original series; lower portion (*italics*) = filtered series. The abbreviations refer to series to catch of Mazatlán (M) and Guaymas (G), and blue shrimp, *Litopenaeus stylirostris* (a); white shrimp, *L. vannamei* (b); brown shrimp, *Farfantepenaeus californiensis* (c), and catch for trip (cv). The other abbreviations refer to climate series, Pacific Decadal Oscillation (PDO) and Multivariate El Niño Index (MEI), finally pluvial precipitation (P) and fluvial discharge (F), in the warm (w) and cold (c) periods. Numbers in bold indicate significant correlation ($p < 0.05$).

	Ma	Mb	Mc	Ga	Gc	Gcv	PDOc	PDOw	MEIc	MEIw	Pc	Pw	Fc	Fw
Ma		0.4	–0.2	**0.6**	0.4	0.5	**0.6**	0.4	–0.2	0.2	0.0	–0.1	–0.2	–0.4
Mb	*0.4*		0.2	**0.6**	0.5	0.5	0.2	0.5	–0.2	**0.6**	0.0	–0.5	0.0	–0.4
Mc	*–0.3*	*–0.2*		0.0	0.2	0.2	0.0	0.3	0.2	0.3	–0.4	–0.2	–0.3	0.0
Ga	***0.8***	***0.8***	*–0.4*		**0.6**	**0.6**	**0.5**	0.4	–0.3	0.3	–0.3	–0.2	–0.3	–0.2
Gc	***0.6***	*0.4*	*0.2*	*0.5*		**0.9**	0.4	0.4	–0.2	0.4	–0.2	–0.4	–0.2	–0.4
Gcv	***0.9***	*0.3*	*–0.1*	***0.6***	***0.8***		0.2	0.3	–0.5	0.3	–0.3	–0.1	–0.4	–0.3
PDOc	***0.8***	***0.6***	*0.1*	***0.8***	***0.7***	***0.7***		0.4	0.3	0.1	0.0	–0.3	–0.2	–0.4
PDOw	*0.3*	*0.5*	*0.0*	*0.5*	*0.2*	*–0.1*	***0.6***		0.2	**0.6**	0.2	0.0	0.1	–0.1
MEIc	*–0.3*	*–0.1*	***0.6***	*–0.4*	*0.0*	*–0.4*	*0.0*	*0.3*		0.2	0.4	–0.3	0.3	–0.3
MEIw	*–0.2*	*0.3*	*0.2*	*0.0*	*0.3*	*–0.2*	*0.2*	***0.5***	***0.7***		0.1	–0.1	0.0	–0.2
Pc	***–0.7***	*0.0*	*0.0*	*–0.4*	***–0.5***	***–0.9***	*–0.5*	*0.3*	*0.5*	*0.4*		–0.2	**0.9**	–0.3
Pw	*–0.3*	***–0.7***	*–0.4*	*–0.4*	***–0.7***	*–0.4*	***–0.6***	*–0.2*	*–0.4*	*–0.4*	*0.0*		–0.3	**0.7**
Fc	***–0.8***	*0.1*	*0.1*	*–0.4*	*–0.4*	***–0.8***	*–0.5*	*0.3*	*0.5*	*0.4*	***1.0***	*0.0*		–0.2
Fw	*–0.4*	*–0.3*	*–0.2*	*–0.2*	***–0.8***	***–0.7***	*–0.5*	*0.1*	*–0.3*	*–0.3*	*0.4*	***0.8***	*0.3*	

TABLE 4

Results of the multiple correlation analysis of shrimp catch data at Guaymas, Sonora. Significant results at 5% confidence are shown in bold numbers. In the first column are variable abbreviations. The statistical abbreviations such as β coefficients represent the relative contribution of each independent variable in the prediction; the *t* value and resulting *p* value are used to test the hypothesis; R^2 is the coefficient of multiple determination. Numbers in bold indicate significant correlation ($p < 0.05$).

Guaymas, Sonora				
(a) Blue shrimp (*Litopenaeus stylirostris*)				
	β	B	$t_{(11)}$	*p*
b_0		1467.2	7.4	0.000
PDO_c	**0.789**	**893.1**	**4.1**	**0.002**
F_c	–0.068	–44.9	–0.4	0.731
$R^2 = 0.678$; $F_{(2,11)} = 11.6$; $p < 0.002$				
(b) White shrimp (*L. vannamei*)				
	β	B	$t_{(21)}$	*p*
b_0		2445.6	23.5	0.000
MEI_c	–0.094	–81.0	–0.5	0.653
P_c	**–0.538**	**–448.5**	**–2.6**	**0.017**
$R^2 = 0.353$; $F_{(2,21)} = 5.7$; $p < 0.010$				
(c) Brown shrimp (*Farfantepenaeus californiensis*) (CPUE Data)				
	β	B	$t_{(21)}$	*p*
b_0		0.989	27.208	0.000
PDO_c	**0.554**	**0.172**	**3.980**	**0.001**
P_c	**–0.507**	**–0.172**	**–3.643**	**0.002**
$R^2 = 0.595$; $F_{(2,21)} = 15.4$; $p < 0.000$				

TABLE 5

Results of the multiple correlation analysis of shrimp catch data at Mazatlán, Sinaloa. Significant results at 5% confidence are shown in bold numbers. In the first column are the variable abbreviations. The statistical abbreviations such as β coefficients represent the relative contribution of each independent variable in the prediction; the *t* value and resulting *p* value are used to test the hypothesis; R^2 is the coefficient of multiple determination. Numbers in bold indicate significant correlation ($p < 0.05$).

Mazatlán, Sinaloa				
(a) Blue shrimp (*Litopenaeus stylirostris*)				
	β	B	$t_{(13)}$	*p*
b_0		3859.4	25.832	0.000
PDO_c	**0.670**	**887.1**	**5.586**	**0.000**
P_c	**–0.443**	**–483.6**	**–3.692**	**0.003**
$R^2 = 0.832$; $F_{(2,13)} = 32.2$; $p < .00001$				
(b) White shrimp (*L. vannamei*)				
	β	B	$t_{(13)}$	*p*
b_0		1043.9	5.7	0.000
PDO_c	**0.744**	**831.4**	**4.3**	**0.001**
P_c	**0.615**	**566.3**	**3.5**	**0.004**
$R^2 = 0.642$; $F_{(2,13)} = 11.7$; $p < 0.001$				
(c) Brown shrimp (*Farfantepenaeus californiensis*)				
	β	B	$t_{(13)}$	*p*
b_0		1977.4	31.4	0.000
MEIc	**0.779**	**310.9**	**3.2**	**0.007**
P_c	–0.476	–130.1	–1.9	0.073
$R^2 = 0.442$; $F_{(2,13)} = 5.1$; $p < 0.023$				

resulting correlations, using only the two variables displaying the highest weight, are shown in Tables 4 and 5. Using only those two variables, we estimated forecasted landings which were then compared to actual data.

RESULTS

Table 3 shows the results from the cross-correlation analysis between catch time series and environmental variables summarized in two correlation matrices. The upper and lower matrices show the correlation between original and filtered (*italics*) data, respectively. The lower matrix, which shows a higher proportion of significant results, indicates that most catch series are significantly correlated with the cold season (January–June) PDO (PDO_c), P_c, MEI_c and F_c; PDO_c was positively correlated with shrimp catch; whereas rainfall was negatively correlated, except for white shrimp landed at Mazatlán which had a significant negative correlation with rainfall and river flow (P and F).

The results of multiple correlation analysis between catch and the two best fit variables are shown in Tables 4 (for Guaymas) and 5 (for Mazatlán); the name of each variable and values of the equation and weighed beta coefficients, as well as *t* and *p* values for the test of hypothesis, are shown; b_0 is not.

The comparison between forecasted and actual catch values for Guaymas is displayed in Figure 2. In the case of blue shrimp (fig. 2A), a declining trend is evident between 1988 and 1991, with the lowest values during 1991–1992. This trend may be related to the cold period mentioned by Lavín et al. (2003); from 1991 landings rise steadily to peak in 1996–1997, thereafter dropping towards the end of the period. In the case of blue shrimp, PDO_c and F_c account for ca. 70% of total variability ($R^2 = 0.678$), with PDO_c contributing the most ($\beta = 0.789$).

Catch and CPUE data for brown shrimp at Guaymas were analyzed in two stages: first, when landings data were related to rainfall during the cold season (P_c; $\beta = 0.538$); and second, when landings data were related to MEI for the cold season ($\beta = 0.094$). Both account for only 35% of variability (fig. 2B). In a second stage, CPUE data were analyzed revealing that the cold-season variables PDO_c and P_c had similar weight as did the predictors (0.554 and –0.507, respectively), and altogether account for 59% of variability (fig. 2C).

In the three cases above, the variables had an influence on landings during the cold season. It is also evident that flow and rainfall during the cold season negatively correlate to landings and CPUE. Figure 2A-C shows the relationship between observed and calculated data; residuals show the differences between both series, highlighting the low catches after the El Niño event of 1982–1983 and the La Niña in 1989–1991.

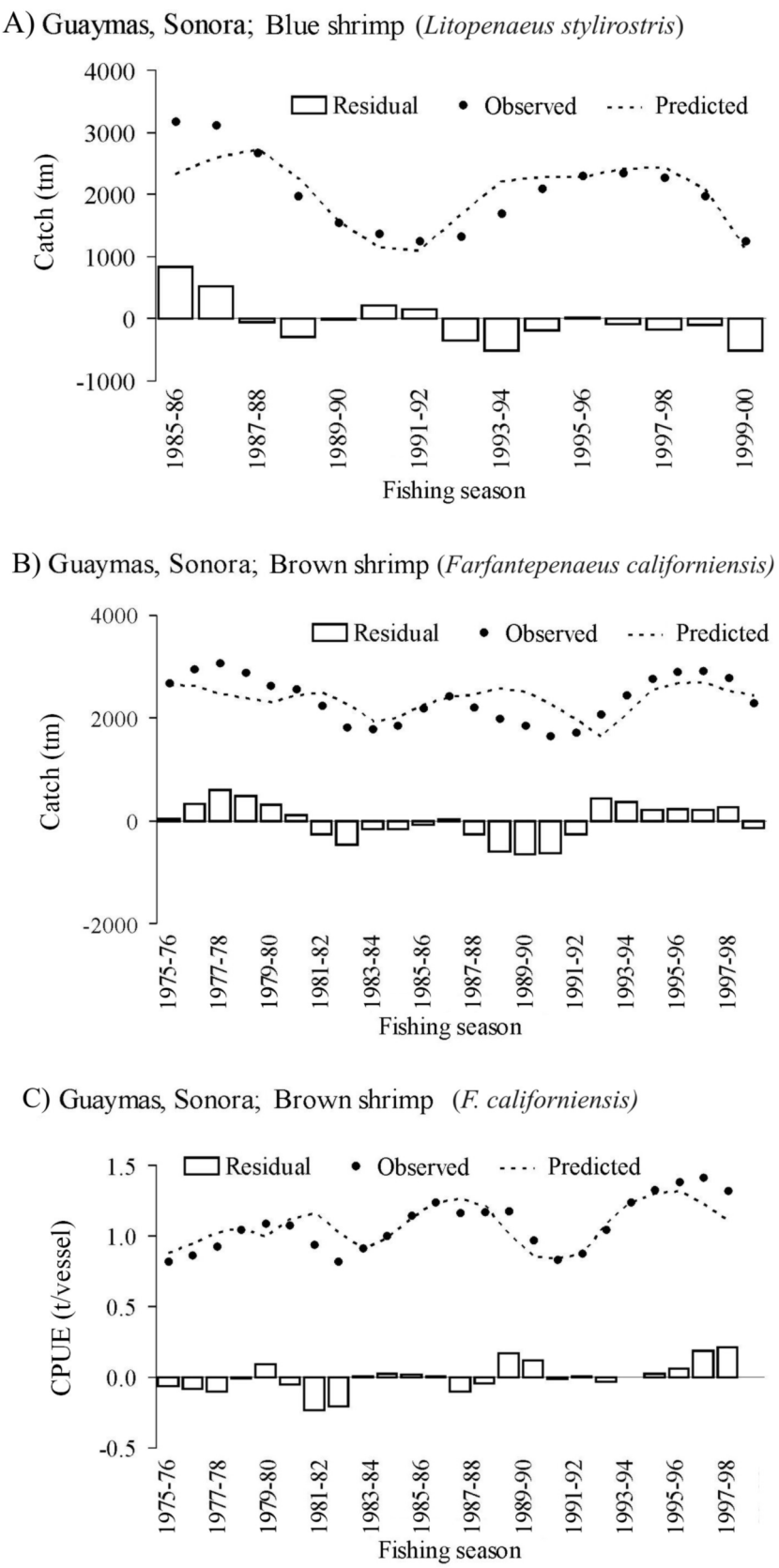

Figure 2. Observed and calculated shrimp catch in metric tons from Guaymas, Sonora, for the fishing seasons 1975–76 through 1999–2000; (A) blue shrimp (*Litopenaeus stylirostris*); (B) brown shrimp (*Farfantepenaeus californiensis*); and (C) catch per unit of effort (CPUE) of brown shrimp.

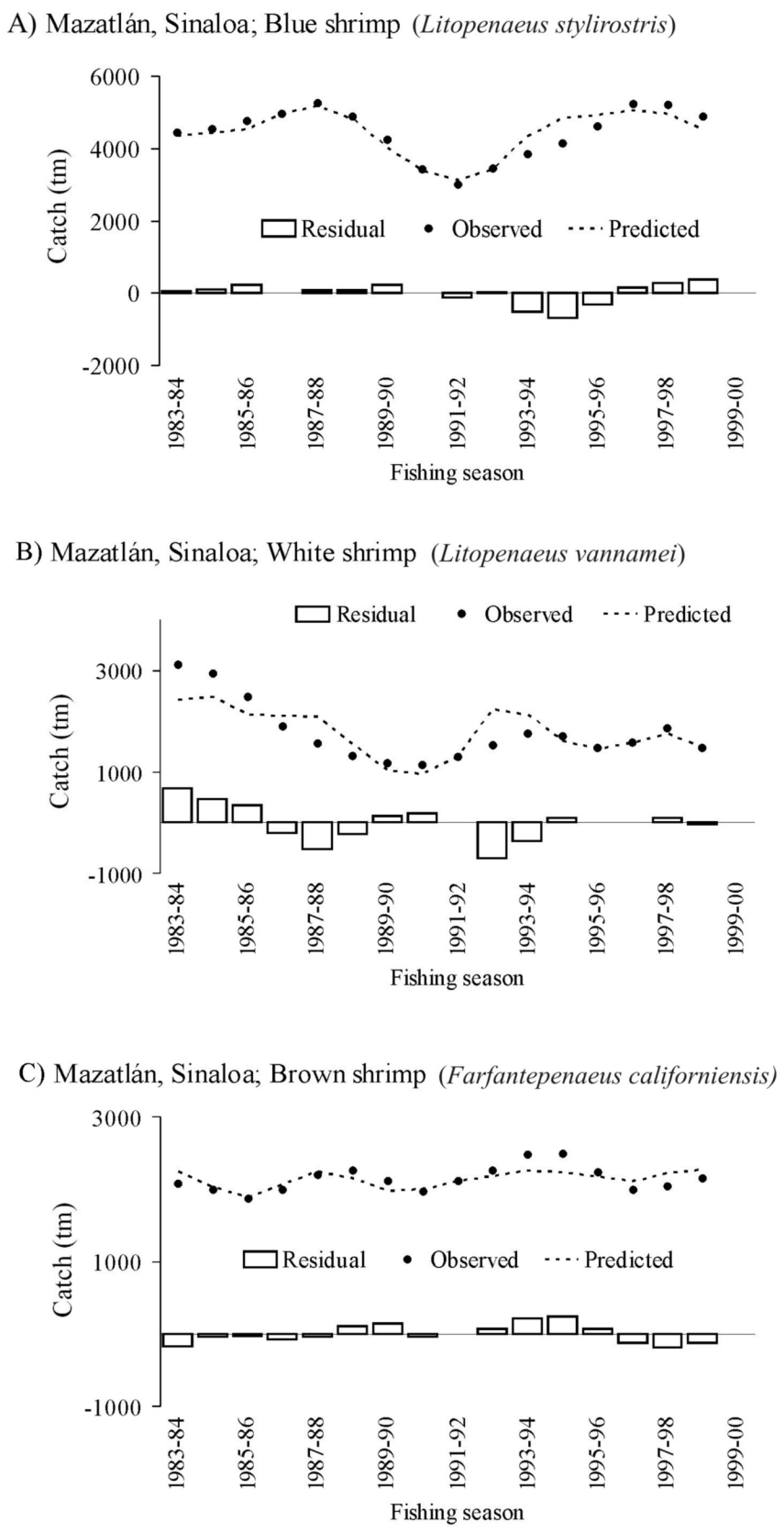

Figure 3. Observed and calculated shrimp catch in metric tons from Mazatlán, Sinaloa, for the fishing seasons 1983–84 through 1999–2000; (A) blue shrimp (*Litopenaeus stylirostris*); (B) white shrimp (*L. vannamei*); and (C) brown shrimp (*Farfantepenaeus californiensis*).

TABLE 6
Reproduction periods of the major shrimp species harvested in the Gulf of California and the source documents.

Blue shrimp (*Litopenaeus stylirostris*)		
Agiabampo	May–July	(Aragón-Noriega 2005)
Guaymas	July–August	(Sepúlveda-Medina 1991)
Mazatlán	June–July	(Sepúlveda-Medina 1991)
Brown shrimp (*Farfantepenaeus californiensis*)		
Guaymas	March–May October–November	(Leal-Gaxiola et al. 2001)
Guaymas-Mazatlán	May–September	(Sepúlveda-Medina 1991)
Agiabampo	June–July October–November	(Romero-Sedano et al. 2004)
Agiabampo	May–August	(Valenzuela-Quiñonez et al. 2006)
White shrimp (*L. vannamei*)		
Mazatlán	May–September	(Sepúlveda-Medina 1991)
Guaymas	June–August	(Sepúlveda-Medina 1991)

Results of the Mazatlán data analyses are shown in Figure 3. Again, the main variable associated with landings is PDO for the cold season ($\beta = 0.670$), followed by rainfall for the cold season (P_c; $\beta = -0.443$). Together, they account for 83% of the variability, similar to the findings for the same species at Guaymas. Results for white shrimp (fig. 3B) indicate that the two variables with the highest likelihood to be related to harvest also correspond to the cold season and are PDO_c and rainfall (P_c). However, these variables have a similar weight (0.744 and 0.615, respectively); the difference in most cases is that harvest is positively correlated with rainfall. The results for brown shrimp (tab. 5 and fig. 3C) are similar to those obtained for the same species at Guaymas, highlighting MEI_c and P_c as the two most important variables ($\beta = 0.779$ and -0.476, respectively).

DISCUSSION AND CONCLUSIONS

Our results indicate that environmental conditions for the first semester of the year (roughly corresponding to the cold season) may influence shrimp production in the Gulf of California during the following fishing season. The reproduction period which results in the recruitment which sustains the fishery was found to occur during the first semester; these findings agree with those from other investigations which are summarized in Table 6.

In most cases, the main reproduction period seems to take place during the first half of the year, and seems to depend on temperature (Aragón-Noriega and Alcántara-Razo 2005). When they compared the data from ripe females between northern and southern sites in the study area, these authors found that a well-defined peak of reproductive activity is evident at the north, where the mean SST is 22.6°C, whereas at the south, where mean

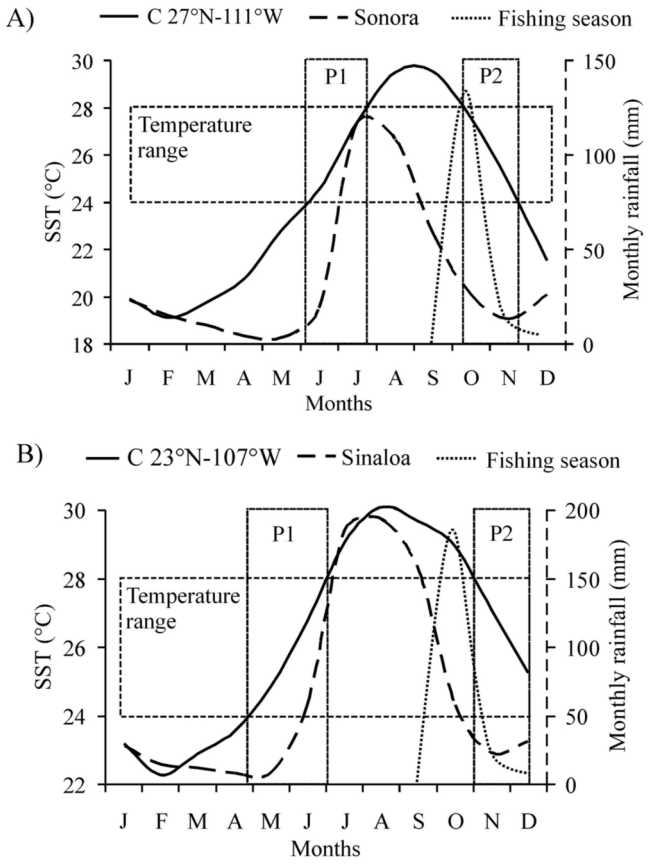

Figure 4. Seasonal SST cycles in two quadrats located at 25°and 27°N, and rainfall cycles in the Sinaloa (upper line) and Sonora (bottom line) coastal basins. The two reproduction periods reported for the three major shrimp species (blue shrimp, *Litopenaeus stylirostris*; white shrimp, *L. vannamei*; and brown shrimp, *Farfantepenaeus californiensis*) are depicted, along with catches during the fishing season.

SST is 26.2°C, the reproductive activity takes place throughout the year.

A conceptual model of the seasonal processes in the shrimp life cycle which includes seasonal variation in SST and rainfall, reproduction periods, and fishing season, is shown in Figures 4A (Sonora) and 4B (Sinaloa).

It is worth noting that the fishing season is relatively long, between September and March of the following year, but most of the harvest is caught during the first two to three months. However, the fishing areas of the two fleets (Guaymas and Mazatlán) during the first part of the fishing season are considered to be very similar because vessels generally congregate in areas of higher shrimp density and scatter steadily towards other areas as the fishing season progresses. A key aspect in the analysis is temperature tolerance by the three shrimp species, which seemingly ranges between 24° and 28°C (Sierra et al. 2000).

Figures 4A and 4B illustrate that the first reproduction peak may be related to the ascending portion of SST, from late April in the Mazatlán area and from June farther north; a second peak of reproductive activity

could occur between October and December, when SST is declining. Theoretically, the optimum SST for reproduction would be ~26°C.

If the above are true, most shrimp harvested by the Guaymas and Sonora fleets are likely from the first reproduction period, which in the case of brown shrimp gives rise to the so-called spring cohort (López-Martínez et al. 2002); the second reproduction period during the last months of the year apparently gives rise to a second cohort (fall cohort), which is important because it represents the reproductive population for the following year.

The above might explain the relationship between shrimp catch and PDO during January–June, since the influence of the north Pacific Ocean weather becomes evident as SST decreases as a result of cold weather and strong winter winds (Bernal et al. 2001). During an anomalous cold period, the reproductive activity declines as ripening processes get slower and the reproduction season becomes shorter, which results in low recruitment (Leal-Gaxiola et al. 2001; Aragón-Noriega and Alcántara-Razo 2005).

Strong warm events like those in 1982–1983 and 1997–1998 also seem to exert a negative effect on shrimp catches, probably because growth and recruitment are affected when temperature exceeds the upper limit of shrimp's thermal tolerance (López-Martínez et al. 2002).

Our findings indicate that winter rainfall (P_c) is a another factor to consider and has a negative correlation with shrimp harvest; however, winter rainfall is generally scarce, so that its influence may be relatively modest. There is the possibility that this is an indirect correlation, derived from a certain degree of correlation between PDO_c and P_c (see Table 3).

We conclude that the influence of weather during the cold season, between January and June, accounts for a significant proportion of blue shrimp catches in Guaymas and Mazatlán, which, in terms of planning, might provide a suitable forecast tool for the fishing industry.

ACKNOWLEDGEMENTS

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THE LIFE HISTORY AND ECOLOGY OF BLACK CROAKER, *CHEILOTREMA SATURNUM*

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ABSTRACT

Results from spatial and temporal distribution analysis of 5,157 black croaker (*Cheilotrema saturnum*) collected by gillnet from 1995–2004 at stations from Newport to Santa Barbara, California, including Santa Catalina Island, indicated that peak catch per unit effort (CPUE) occurred along the Palos Verdes Peninsula. Annual gillnet CPUE was greatest in 2000. The highest black croaker abundance was recorded in 1997 using standardized impingement data from two Santa Monica Bay generating stations. Length-frequency analyses from both gill net and impingement sampling indicated that a large proportion of black croaker were small in size immediately prior to and during the 1997–98 El Niño Southern Oscillation, and then increased in size with time. Observed black croaker ages ranged up to 21 years old, with most fish less than 14 years old. Von Bertalanffy growth parameters were L_∞ = 237.7, k = 0.31, t_0 = –1.778, and N = 779, with no significant differences between the sexes. Gonosomatic indices peaked in June, followed by August, suggesting late-spring to summer spawning. Mortality adjusted hindcasting indicated that peak recruitment occurred in 1997.

INTRODUCTION

Sciaenids comprise significant portions of the nearshore ichthyofauna within the Southern California Bight (SCB), accounting for six of the ten most abundant species observed from August 1996 to June 1998 (Pondella and Allen 2000). Black croaker (*Cheilotrema saturnum*) ranked as the fourth most abundant species along the mainland during this study. Although highly abundant, black croaker was the only member of the family common to coastal southern California that does not support either a targeted recreational or commercial fishery (Limbaugh 1961; Love et al. 1984). Black croaker reach a maximum size of 381 mm standard length (SL) and range from Magdalena Bay, Baja California Sur, Mexico, to Point Conception, California. They occur from the surface to depths of 45 m, with the greatest concentrations in depths from 3–15 m (Limbaugh 1961; Miller and Lea 1972; Feder et al. 1974; Love et al. 2005). Principal habitat consists of open coast rocky reefs and coastal embayments throughout their range, with adults occasionally observed over sand patches during the summer (Limbaugh 1961; Quast 1968; Feder et al. 1974; Allen 1985). In waters with low turbidity, adults have been observed in large caves or crevices within the reef, while in murky conditions aggregations have been observed at 3 m above the bottom (Limbaugh 1961). Undoubtedly, black croaker comprise an important component of the nearshore rocky-reef ichthyofauna in the SCB (Stephens et al. 2006).

Most demographic population models, such as the Adult Equivalent Loss (AEL) and Fecundity Hindcasting (FH), require multiple life-history parameters, including some estimation of longevity, age and growth, mortality, and spawning seasonality (Parker 1980; Jensen et al. 1982; Saila et al. 1997; Lo et al. 2005; Newbold and Iovanna 2007). While many of these life-history parameters have been determined for commercially important species, such as northern anchovy (*Engraulis mordax*) (Hunter and Macewicz 1980; Hunter and Goldberg 1980; Butler et al. 1993), similar effort has not been expended on exclusively recreational species, and even less has been applied to forage species. Interest in analyzing the potential effects of non-fishing anthropogenic uses of coastal marine waters (wastewater discharges, power plant once through cooling, storm-water runoff, etc.) has focused more on species that either exclusively support recreational fisheries or function as forage species, such as black croaker. Assessments were often limited by the life-history parameters available, such as during the recent assessment of the cooling water system at Huntington Beach Generating Station (MBC and Tenera 2005[1]).

Despite the need to understand anthropogenic effects and its abundance within the SCB, little research has been conducted on black croaker. Published research has been limited to preliminary information on the life-history and ecology (Limbaugh 1961) and an assessment of spawning seasonality (Goldberg 1981). To better un-

[1]MBC Applied Environmental Sciences and Tenera Environmental. 2005. AES Huntington Beach Entrainment and Impingement Final Report, April 2005.

derstand black croaker demographics and population abundance trends, life-history parameters must be described. This study was undertaken to document aspects of the life-history parameters of black croaker, e.g., age at length, the length-weight relationship, reproductive biology and seasonality for both sexes, spatial distribution throughout the SCB, an examination of population trends over time, and recruitment trends. While black croaker is not the subject of any species-specific fishery management plan, its perceived role in the ecosystem may become important with a shift towards ecosystem-based fishery management, such as in marine protected areas. This study aims to provide greater understanding of the life-history parameters of one member of the rocky-reef community.

MATERIAL AND METHODS

Collection of Specimens

Individual black croaker were collected using experimental gillnets as part of the California Department of Fish and Game's monitoring via the Ocean Resource Enhancement and Hatchery Program (OREHP) (Pondella and Allen 2000). From 1995–2004 experimental gillnets were set overnight at seven stations along the California coast; Santa Barbara, Ventura, Malibu, Palos Verdes, Seal Beach, and Newport (fig. 1). Three stations were occupied at Santa Catalina Island, California, including the west and east ends of the island as well as Catalina Harbor. Due to low abundance, all data from island stations were summed together as Santa Catalina Island. Sampling occurred annually in April, June, August, and October from 1995 through 2004. Ventura, Malibu, Palos Verdes, Seal Beach, and Newport were sampled in all years. Santa Barbara and the Santa Catalina stations were sampled beginning in August 1996. Sampling at Marina del Rey (the third Santa Catalina station) began in October 1996. All stations were sampled continuously thereafter.

All nets at the open coastal stations were set perpendicular to the shoreline. Six horizontal gillnets were set on the bottom at each station from dusk to dawn. Each net was 45.7 m long and 2.4 m deep, with two sets of three different-sized mesh panels (25.4 mm, 38.2 mm, and 50.8 mm square mesh). All nets were set in 5–14 m of water just outside of the surf zone, typically adjacent to kelp beds or the fringe of rocky reefs. Exceptions were Marina del Rey and Seal Beach, which have neither kelp beds nor rocky reefs. At Marina del Rey, a private boat marina, nets were set outside of the vessel traffic lanes at two sites, parallel to the rip-rap between the U.S. Coast Guard and University of California, Los Angeles docks and perpendicular to the shoreline at Mother's Beach. At Seal Beach, nets were set parallel near the west jetty just downcoast of the Seal Beach Pier.

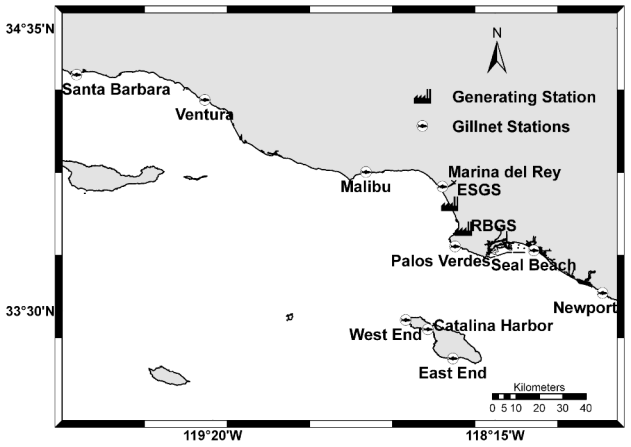

Figure 1. Map depicting all gillnet and power plant sampling locations for black croaker (*Cheilotrema saturnum*) study during 1995–2004.

From April 1995–August 2001 and October 2003–October 2004, all samples were measured to the nearest 5 mm unit SL. Beginning in October 2001 through August 2003, all samples were measured to the nearest millimeter for SL, fork length (FL), head length (HL), and total length (TL), and weighed to the nearest gram (g), sexed macroscopically, while gonads were weighed to the nearest 0.5 g, and sagittal otoliths were removed.

Distribution

Spatial CPUE was calculated as the total annual abundance caught divided by the total number of monthly sampling events for that year. Temporal CPUE represents the monthly mean of catch per net across all sampled stations. Differences among spatial and temporal CPUE were each tested with a one-way analysis of variance (ANOVA) with a Tukey post-hoc test. Prior to the ANOVA, both CPUE data sets were transformed using $\ln(x+1)$ to satisfy the assumption of normality, which was confirmed using a Shapiro-Wilk w statistic (Legendre and Legendre 1998). Temporal CPUE was also tested for correlation with mean monthly sea surface temperature (SST) as recorded at Newport Pier (www.sccoos.org). Data from Newport Pier were used rather than Santa Monica Bay because they were collected more consistently during April 1995 through October 2004.

Standard lengths of gillnet-collected fish were combined and divided into 25 mm SL size classes for length-frequency analysis. The mean standard lengths by site and annual mean standard lengths were compared individually using an ANOVA with a Tukey post-hoc test. Pearson one-tailed correlation was used to test the relationship between mean summer SST and mean annual SL.

Additional long-term (1979–2006) inter-annual variation was examined using impingement records from the Redondo Beach and El Segundo Generating Stations, California (fig. 1). The Redondo Beach Generating Station withdraws seawater from two intake structures

within King Harbor; one located 600 m offshore near the end of the breakwater at the mouth of the harbor at a depth of 13 m and the other located 305 m offshore, but within the harbor, at a depth of 9 m. The El Segundo Generating Station withdraws seawater through two cooling-water structures located approximately 790 m offshore in Santa Monica Bay at a depth of 9 m. Abundances recorded during heat treatments were standardized to annual cooling-water flow volumes in billions of gallons (bg). For a complete description of heat treatment impingement see Miller (2007). Pearson one-tail correlation analysis was used to test the relationship between annual impingement and mean annual SST.

Age, Growth, and Morphometrics

Relationships between head, fork, and total length to standard length were described via linear regression. The length-weight relationship was examined by fitting the relationship: $W = aL^b$, where W = weight in grams, L = standard length in mm, and a and b are constants determined by nonlinear regression.

Saggital otoliths were removed from all individuals collected from October 2001–August 2003. Each otolith was cleaned, air-dried, and stored in a pre-labeled coin envelope in the field. Each right otolith was mounted on a wood block with cyanoacrylate glue and sectioned on the transverse axis through the focus using a Buheler Isomet™ low-speed saw (Allen et al. 1995). A thin section (0.7 mm) was cut using two diamond-embedded blades (Allen et al. 1995). Sections (N = 825) were viewed in a black-bottomed watch glass filled with water and read under a stereoscope at 25× magnification using reflected light. Each otolith was read twice by a single reader, at least four months apart. The value from two concordant readings was accepted as the best estimate of age. When necessary, a third reading was made when two consistent values were not obtained. In the event agreement could not be reached, the sample was excluded from further analyses. Otolith edge analysis was used to confirm the seasonal deposition consistent with annuli formation. Lengths at age were estimated by deriving the mean standard length for each age class based on the otolith analysis. These data were visualized using the von Bertalanffy growth model using VONBIT (FAO 2005):

$$L_t = L_\infty (1 - \exp - k^{(t-t_0)}),$$

where:

L_t = length at time t;
L_∞ = theoretical maximum length;
k = constant expressing the rate of approach to L_∞; and
t_0 = theoretical age at which $L_t = 0$.

Von Bertalanffy models were constructed for all individuals combined and by sex; immature or sex undetermined individuals were excluded from the sex-specific analysis. The differences between sex-specific growth were tested by an analysis of residual sum of squares derived by non-linear regression (ARSS; Haddon 2001).

Reproduction and Recruitment

Sex distributions and gonosomatic indices were derived from 897 individuals collected during gillnet sampling from 2001–03. Deviation from an expected gonochoric sex ratio of 1:1 was tested with a X^2 analysis. Gonosomatic index (GSI) values were derived by the following (Barbieri et al. 1994):

GSI = (Gonad Weight / (Gonad Free Body Weight)) x 100.

Differences in monthly GSI values were tested using a one-way ANOVA for each sex.

Annual recruitment was estimated using both standardized generating station impingement and gillnet abundances. Year-class abundances were drawn from the current age and growth study. Catch-curve analysis was used to estimate instantaneous mortality (Z) (Haddon 2001). Abundances by year class were plotted independently for the 2002 and 2003 collections. Due to the lack of a sustained fishery (commercial or recreational), $Z \approx M$ (Haddon 2001). Hindcasted annual recruitment was estimated by adjusting the age-class abundance for each year by the following (Allen et al. 1995):

$$N_t = N_0 (1/S)^t$$

where:

N_0 = number of fish in a year class at t = 0;
N_t = estimated number of recruits at t years in past corrected for mortality; and
S = annual estimated survivorship.

Total year-class recruitment estimates represent the summation across estimates calculated for each collection year. Recruitment success over time was estimated from recorded lengths of fish impinged at Redondo Beach Generating Station and El Segundo Generating Station. Abundances of young-of-year (YOY) individuals, as determined by the current age-at-length study (<151 mm SL), were standardized to the annual cooling-water flow (bg). Pearson one-tailed correlation analysis was used to test the relationship between SST and each recruitment index (hindcasted and impingement). The potential relationship between kelp canopy coverage along Palos Verdes Peninsula coastline (MBC 2006[2]) was compared with mortality-corrected hindcasted recruitment with a Pearson one-tailed correlation analysis. We also tested the relationship between the standardized

[2]MBC Applied Environmental Sciences. 2006. Central Region Kelp Consortium annual report.

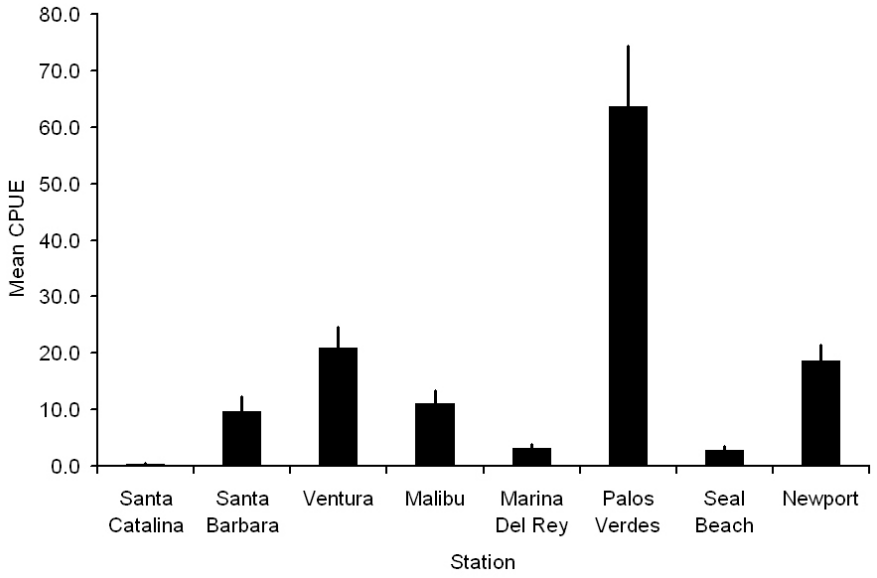

Figure 2. Mean gill net catch per unit effort (CPUE) of black croaker (*Cheilotrema saturnum*), plus one standard error, by gill net station, 1995–2004.

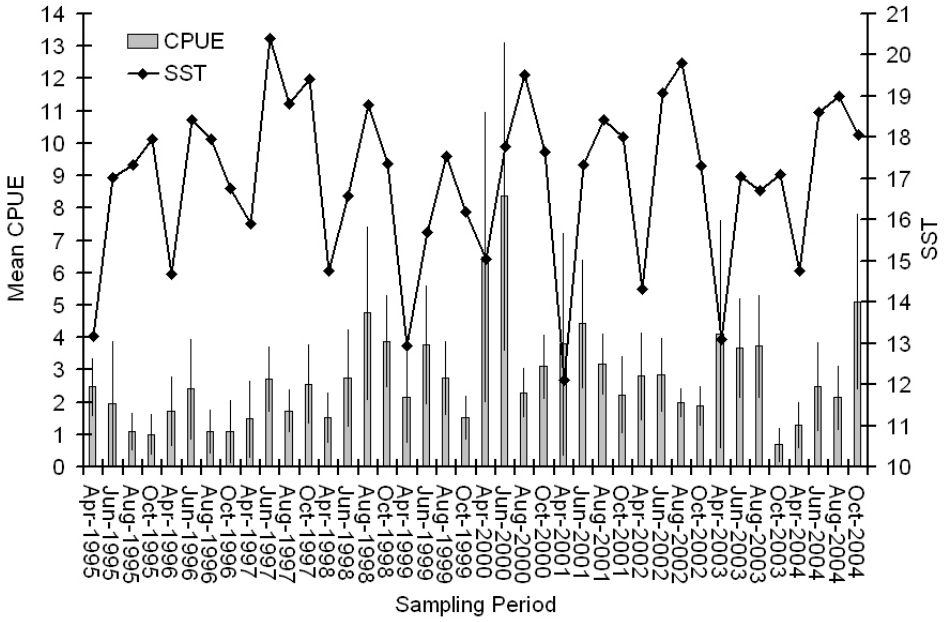

Figure 3. Mean monthly gill net catch per unit effort (CPUE) of black croaker (*Cheilotrema saturnum*) plus standard error, and mean monthly summer sea surface temperature (SST) for all sampling periods, 1995–2004.

YOY impingement abundance and mean summer (June–September) surface chlorophyll-*a* concentration recorded at Station C8 of the Point Loma Ocean Outfall monitoring array (fig. 1) as reported by SCCOOS (www.sccoos.org). Chlorophyll-*a* densities were only available from 1998 on, which only allowed four years of overlap with the hindcasted data. Therefore, no comparisons were attempted. All statistical tests used were executed with SPSS 15 for Windows Grad Pack.

RESULTS

Distribution

A total of 5,157 individuals were collected during gillnet sampling. The catch at Palos Verdes was significantly higher (ANOVA, $F = 32.328$, df = 7, 69, $p < 0.001$) than all other sites, with greater than 60 fish/survey (fig. 2). Ventura and Newport Beach were the next most populous, each with approximately 20 fish/survey observed

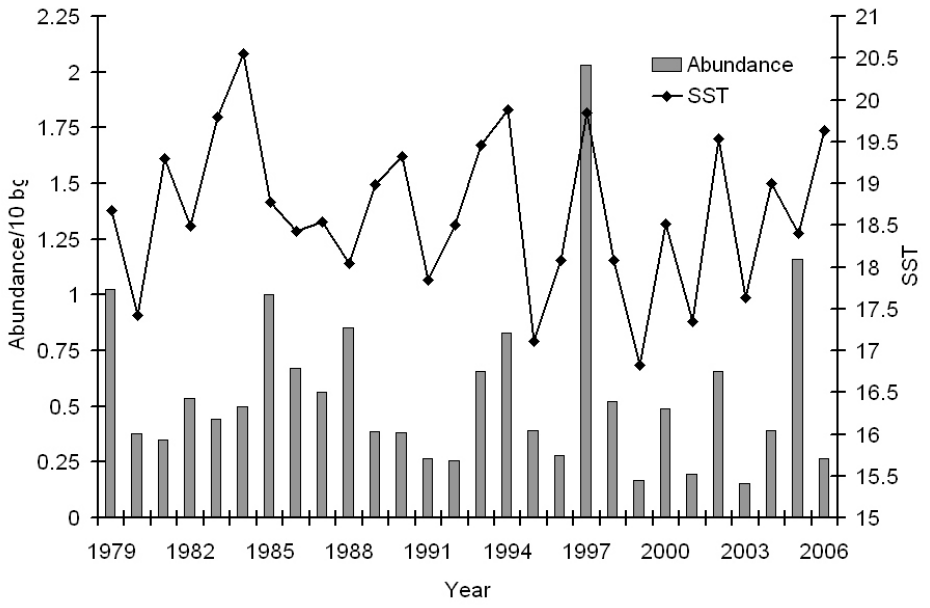

Figure 4. Total abundance of black croaker (*Cheilotrema saturnum*) per 10 bg of cooling water circulated at Redondo Beach Generating Station and El Segundo Generating Station, and mean summer Newport SST (°C), 1978–2006.

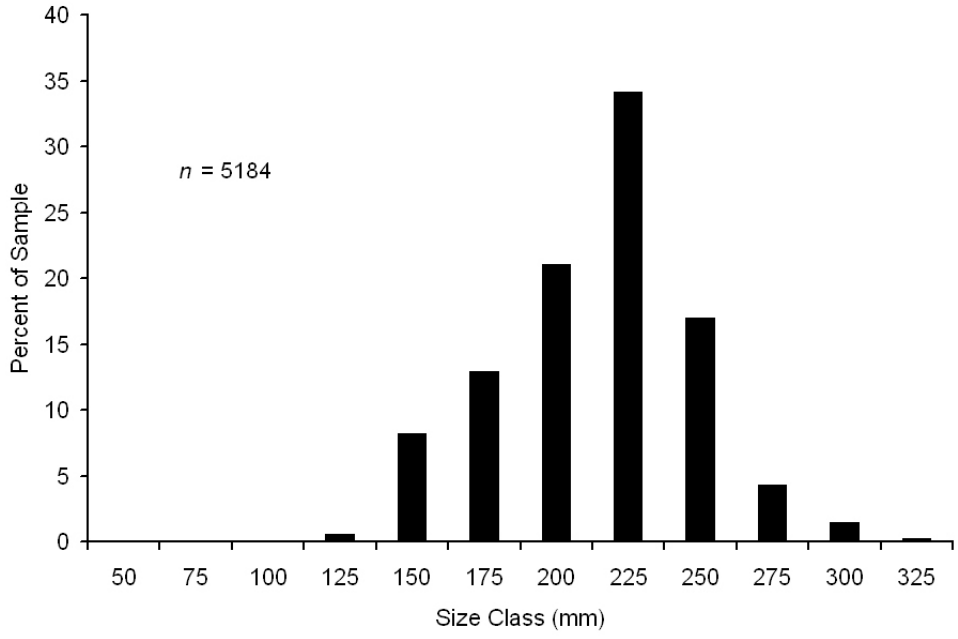

Figure 5. Percent of total gill net catch of black croaker (*Cheilotrema saturnum*) per 25 mm SL size class for all surveys, 1995–2004.

during the study period. Catch per unit effort at each of the remaining coastal sites was observed, on average, to be less than 11 fish/survey. Santa Catalina Island collections were minimal, with less than 0.5 fish/survey on average. Temporal collections were not significantly different ($p = 0.80$), although landings peaked in April and June 2000, with six and eight fish/station, on average, respectively (fig. 3). The lowest catch was recorded in October 2003, with 0.6 fish/station, on average. Catch per unit effort was generally higher from 1998–2003 than during earlier and later periods of the survey. Cumulative impingement abundance was highly variable with a general downward trend over time (fig. 4). Abundances varied relatively consistently with SST ($r = 0.37$, $p = 0.03$), with peak abundance in 1997 at better than 2 fish/10 bg.

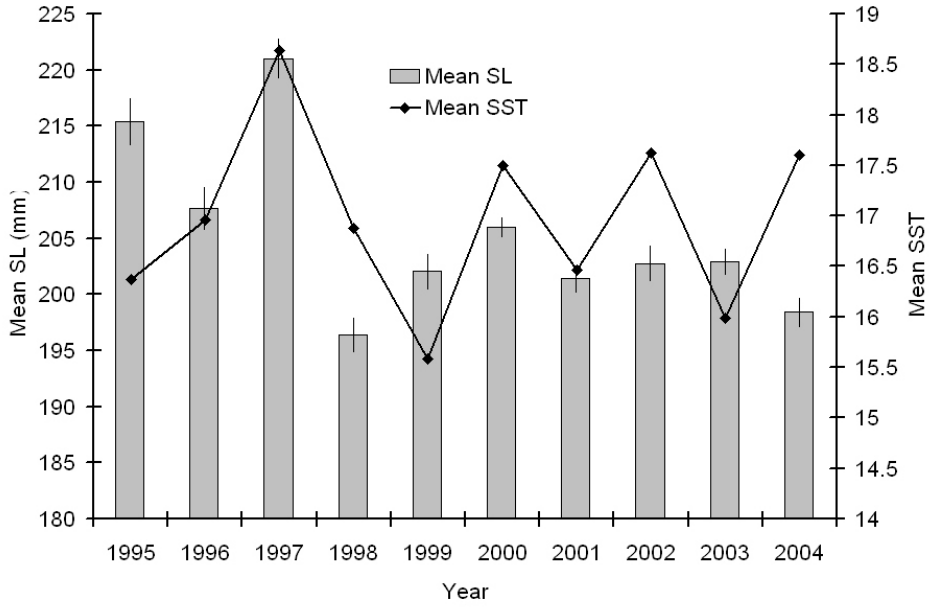

Figure 6. Annual mean standard length (mm), plus standard error, for all gillnet-collected black croaker (*Cheilotrema saturnum*) and mean annual summer sea surface temperature (SST), 1995–2004.

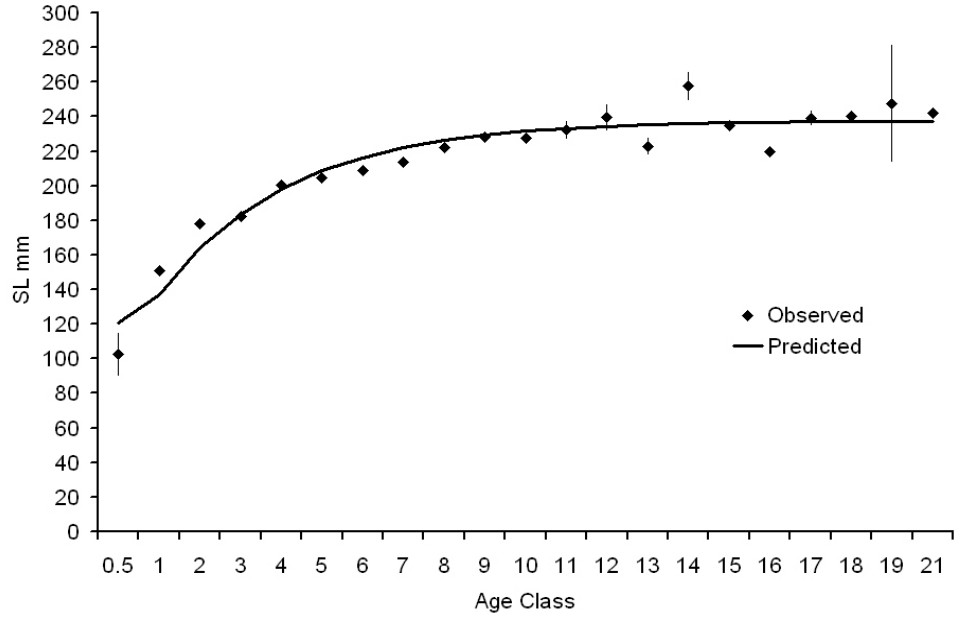

Figure 7. Von Bertalanffy predicted and observed, with standard error, age-at-length curves for all sampled black croaker (*Cheilotrema saturnum*).

Standard lengths of gillnet-collected individuals (n = 5184) ranged from 150 to 250 mm SL with peak abundance in the 225 mm SL size class (fig. 5). Black croaker collected at Santa Barbara were significantly larger than the remaining coastal stations, while Santa Catalina Island collections were significantly larger than those from all coastal stations (ANOVA, F = 60.461, df = 7, 5180, $p < 0.001$). Annual mean standard length was not significantly correlated with annual mean SST (r = 0.39, p = 0.13). Mean lengths were relatively high from 1995 to 1997 before declining precipitously in 1998, then gradually increasing to a plateau in 2001 (fig. 6).

Age and Growth

Relationships between length categories (SL, TL, FL) closely followed a linear distribution (tab. 1). The length-weight distribution fits a curve described by the equation $W = 0\ .00004L^{2.9223}$ (R^2 = 0.95, n = 745). Opaque

TABLE 1
Conversion equations and associated linear fit and sample size for head length (HL), total length (TL), and fork length (FL) to standard length (SL) for black croaker (*Cheilotrema saturnum*).

Measurement	Relation to SL	R^2	N
Head Length	SL = 2.484(HL) + 59.99	0.65	879
Total Length	SL = 0.822(TL) - 0.01	0.94	882
Fork Length	SL = 0.833(FL) + 1.53	0.95	209

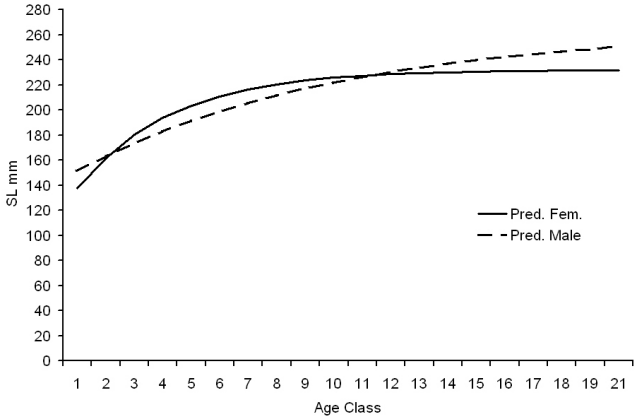

Figure 8. Von Bertalanffy predicted age-at-length curves for male and female black croaker (*Cheilotrema saturnum*).

bands were consistently formed during the spring, and translucent bands in the summer extending into fall, consistent with annual formation. The oldest fish was a 21-year-old male from Santa Catalina Island, which was small for the age but numerous readings were consistent. Nearly 97% of all fish were 13 years old or less, with most fish between five and seven years old and only 25 individuals greater than 14 years old (tab. 2). The largest fish in the data set (324 mm SL) was a 20-year-old male collected at Santa Catalina Island in 2002. The growth rate was steepest from Age-0 to Age-V (fig. 7). Male and female growth rates were not significantly different (fig. 8, ARSS, $F = 3.15$, df = 1,702, $p = 0.08$).

Reproduction

Males comprised a significantly (X^2, $F = 6.581$, df = 1, $p = 0.01$) greater proportion of the total observed gillnet collection. Greater than 60% of individuals collected at Malibu and Marina del Rey were male. Juveniles were collected at all coastal sites except Malibu and Marina del Rey. Both sexes were present in all age classes between 1 and 13, although males represented a measurably greater proportion among most age classes. Females accounted for substantially greater than 50% of the abundance in the 8- and 10-year-old age classes. Age-0 fish appeared to be immature, while immature individuals

TABLE 2
Sample size (*n*) and the mean, standard deviation, and range of standard lengths for black croaker by age class for all samples combined and by mature sex. Von Bertalanffy parameters are listed below each group.

Age Class	All Samples				Female				Male			
	n	Mean	SD	Range	*n*	Mean	SD	Range	*n*	Mean	SD	Range
0.5	18	103	55	17–182								
1	56	151	14	130–205	21	154	12	139–180	20	152	17	130–205
2	58	178	23	144–235	24	185	21	148–222	25	177	21	155–235
3	58	182	24	138–238	20	199	22	165–238	20	178	23	150–226
4	83	201	20	161–275	41	200	18	161–253	38	201	23	166–275
5	138	205	20	149–284	59	210	17	173–246	74	202	21	149–284
6	140	209	17	168–281	50	209	12	174–235	84	210	20	168–281
7	49	214	18	178–272	25	221	20	198–272	22	207	12	186–230
8	53	222	14	198–256	17	224	10	204–240	34	221	16	198–256
9	40	228	21	187–288	19	229	23	204–288	21	227	19	187–270
10	27	227	18	203–279	12	224	12	210–248	14	231	23	203–279
11	26	233	28	200–298	10	244	31	210–298	15	221	18	200–257
12	10	240	25	210–272	5	241	29	210–272	5	239	24	210–266
13	6	223	12	209–243	4	227	14	209–243	1	215		
14	4	258	17	233–270	1	233		233–233	2	269	2	267–270
15	3	235	5	230–240	1	230		230–230	2	238	4	235–240
16	1	220							1	220		
17	3	239	8	230–245	1	243		243–243	1	245		
18	1	240							1	240		
19	4	248	69	157–324	2	206	69	157–254	2	290	48	256–324
21	1	242							1	242		
n	779				312				383			
L_∞	237.7				231.4				259			
k	0.31				0.34				0.13			
t_0	–1.78				–2.36				–6.33			

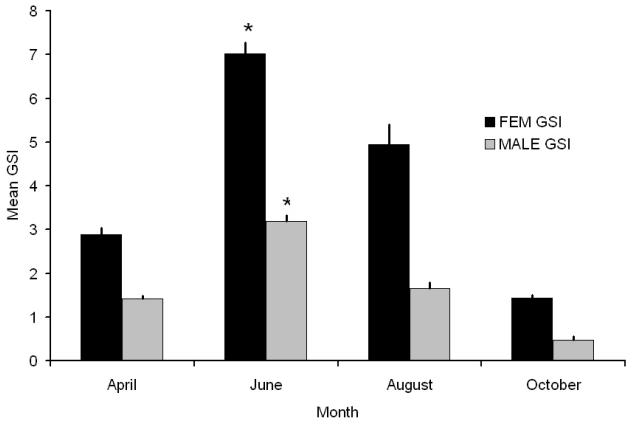

Figure 9. Mean monthly gonosomatic index (GSI), plus one standard error, for male and female black croaker (*Cheilotrema saturnum*). Asterisks denote significant difference.

decreased proportionally in Age-I and Age-II with both sexes showing some maturity during Age-I or at approximately 150 mm SL.

For males, GSI ranged from 0.17 to 8.33%, while female GSI ranged from 0 to 20.48%. Gonosomatic indices were significantly (Kruskall-Wallis, $F = 141.38$, df = 3,893, $p < 0.001$) higher in June samples (females = 7.01, males = 3.19, on average) for both sexes, and remained elevated through August (fig. 9). April indices were measurably elevated compared to October samples.

Year-class strength, unadjusted for mortality, peaked in 1997, with relatively strong abundances in 1996 and 1998 (fig. 10). Mean annual mortality was 0.17 and ranged from $Z = 0.2088$, based on 2002 collections, and $Z = 0.1300$, based on 2003 collections. Mortality-adjusted recruitment indicated that recruitment peaked in 1997, with additional strong year classes in 1982 and 1994. No correlation was found between estimated annual recruitment and mean summer SST ($r = 0.02$, $p = 0.46$), but a significant negative correlation was observed between the presence of the kelp canopy along the Palos Verdes Peninsula and estimated annual recruitment ($r = -0.50$, $p = 0.03$). Analysis of impingement data indicates that peak abundances of young-of-year (YOY) individuals occurred in 1984, 1993, 1994, and with the highest in 1997 (fig. 11). Impingement abundance was significantly correlated with SST ($r = 0.48$, $p = 0.004$) and strongly correlated with mean summer surface chlorophyll-*a* densities ($r = 0.53$, $p = 0.07$).

DISCUSSION

Distribution

Black croaker were primarily distributed along the mainland within the sampling area with few at Santa Catalina Island (fig. 2). This is consistent with the findings of both Pondella and Allen (2000) and Ebeling et al. (1980). Pondella and Allen (2000) recorded black croaker as the fourth most abundant species along the coast, but absent among the 20 most abundant species collected at Santa Catalina Island. In rocky reef surveys along coastal Santa Barbara, California, and nearby Santa Cruz Island dense aggregations of black croaker at the mainland sites were observed while no such aggregations were observed at the island stations (Ebeling et al. 1980).

During the current study, the highest CPUE was recorded adjacent to the rocky reefs around the Palos Verdes Peninsula, with smaller aggregations noted along the rocky reefs of Newport and Ventura (fig. 2). Similar

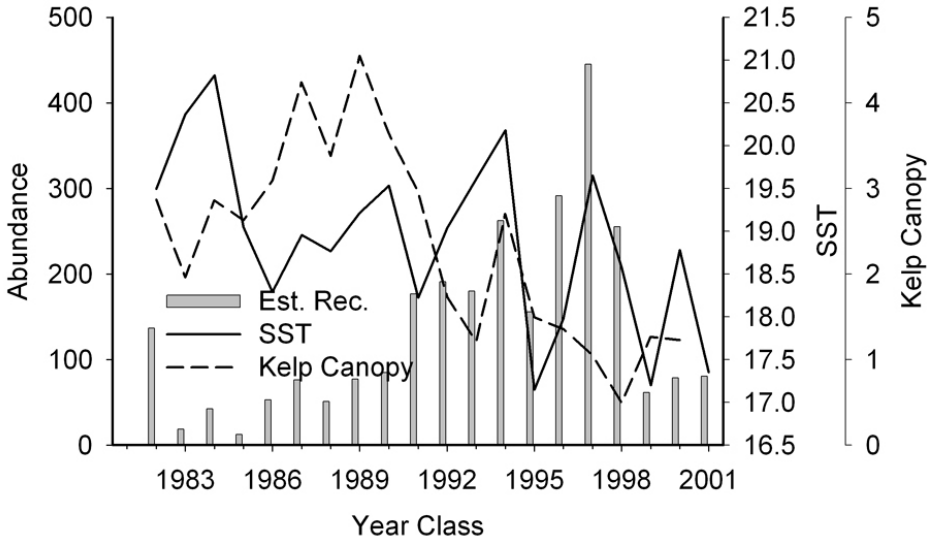

Figure 10. Hindcasted recruitment of black croaker (*Cheilotrema saturnum*), adjusted for mortality, mean annual summer SST, and maximum kelp canopy area (km^2) along the Palos Verdes Peninsula, 1982–2001.

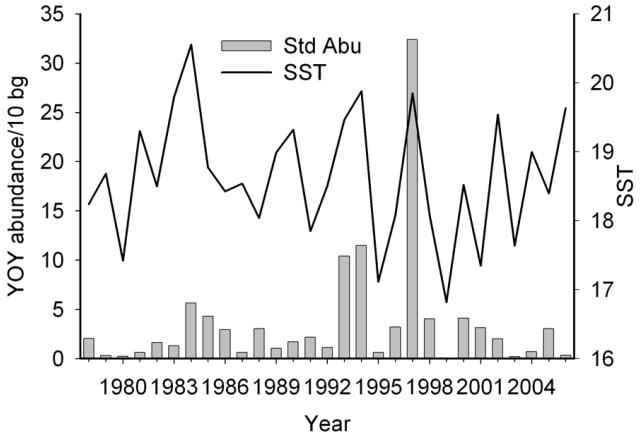

Figure 11. Black croaker (*Cheilotrema saturnum*) young-of-year (YOY) abundance per 10 bg cooling water circulated at Redondo Beach and El Segundo Generating Stations, and mean annual summer Newport SST (°C), 1978–2006.

observations were made by Herbinson et al. (2000[3]) in their analysis of long-term (1977–98) impingement data for sciaenids impinged at coastal generating stations ranging from Ormond Beach in Ventura County, California, to San Onofre, California. They reported peak black croaker abundances at the Redondo Beach Generating Station, located proximate to the Palos Verdes Peninsula. The increased presence of rocky reef habitat along the Palos Verdes Peninsula is consistent with the habitat affinity previously described (Limbaugh 1961; Allen 1985; Allen and Pondella 2006). The lowest CPUE values were recorded at Marina del Rey (degraded wetland) and Seal Beach (protected open coast sandy beach), which was also consistent with the reported habitat preferences.

Peak annual CPUE was recorded in 2000, followed by 1998 and 2001 (fig. 3). The peak catch in 2000 was most likely attributable to the increased availability of individuals recruiting during the El Niño Southern Oscillation event of 1997–98. These individuals would have reached a mean length of 150 mm SL within the two year span. At such lengths, individuals became more available to the size selective gillnets, which preferentially collected individuals >100 mm SL in all mesh panels other than the 25.4 mm square mesh panels. Power plant impingement provided greater sensitivity in detecting YOY abundances than these gillnets. This may be due to YOY being more common in areas away from the kelp beds than near them, which could introduce a bias so that abundance estimates for power plant withdrawals are greater than for where the gillnets were set. Impingement monitoring indicated relatively high YOY abundance in 1997, suggestive of a stronger year class (fig. 11).

[3]Herbinson, K. T., M. J. Allen, and S. L. Moore. 2000. Historical trends in nearshore croaker (family Sciaenidae) populations in southern California from 1977 through 1998. SCCWRP Biennial Report 1999-2000. pp. 253–264.

Age and Growth

Otolith edge analysis confirmed annuli formation in black croaker. This was consistent with findings in other sciaenids, such as weakfish (*Cynoscion regalis*) (Lowerre-Barbieri et al. 1994).

The size distribution of collected individuals nearly reached the reported maximum of 381 mm SL, suggesting that we sampled a good representation of the overall age range of black croaker. The growth rate of black croaker was consistent with previous unpublished estimates and evaluations of other nearshore croaker species. Limbaugh (1961) noted unpublished data in which a 14 in. TL (292 mm SL) individual was aged to 20 years using otolith analysis, consistent with ages observed by this study (fig. 7). Love et al. (1984) reported a steadily increasing rate for white croaker (*Genyonemus lineatus*) with a reported maximum age of 12 years (tab. 3). Joseph (1962) provided age estimates, based on scale analysis, of two common surf-zone associated sciaenids, California corbina (*Menticirrhus undulatus*) and spotfin croaker (*Roncador stearnsii*). He reported that both species grow at highly accelerated rates during the first four years and reach maximum ages of eight and ten years, respectively. The growth rates reported by Joseph (1962) were well in excess of those observed for black croaker, but were generally consistent with the results of Love et al. (1984); all three species had reported maximum life spans much less than black croaker. Miller and Lea (1972) report a maximum length of 391 mm SL for white croaker and greater than 680 mm SL for California corbina and spotfin croaker. The substantially larger size and reported inaccuracies of scale-based age estimates

TABLE 3
Published relevant age parameters from other common nearshore marine sciaenids from the Southern California Bight.

Species	Maximum Reported Age	Difference Between the Sexes	Reference	Structure Aged
Cheilotrema saturnum	21	Yes	Current Study	Otolith
Genyonemus lineatus	12	Yes	Love et al. 1984	Otolith
Menticirrhus undulatus	8	NA	Joseph 1962	Scale
Roncador stearnsii	10 and 22	NA	Joseph 1962; VRG unpub. data	Scale; Otolith
Umbrina roncador	15	Yes	Pondella et al. in press	Otolith

for sciaenids (Lowerre-Barbieri et al. 1994) raises some doubt as to the validity of the Joseph (1962) scale-based age estimates.

Reproduction

Gillnet-sampled assemblages indicated that a significant proportion (56%) of the overall population was male. Wilson and Nieland (1994) noted slightly skewed sex ratios in another common sciaenid species. They examined red drum (*Sciaenops occelatus*) populations in the Gulf of Mexico and noted that females were the predominant sex, although not at a statistically significant level. DeMartini and Fountain (1981) observed a slightly higher proportion of males in breeding adult queenfish, but also not at a statistically significant level.

Gonosomatic indices indicate a spring-to-summer spawning season, which is consistent with previous analyses (Skogsberg 1939; Limbaugh 1961; Goldberg 1981). Additionally, peak GSI values observed in June and August are consistent with research reporting that the highest proportion of stage-4 oocytes occurred in July (Goldberg 1981). Furthermore, ichthyoplankton studies offshore of Huntington Beach, California, confirm a late-summer peak spawning season for black croaker; the maximum density of larvae (160 individuals/1000 m^3) was collected in early September and the next highest density of 30 inds./1000 m^3 was collected in June (MBC and Tenera 2005[1]). Although the validity of GSI ratios for assessing reproductive activity has been questioned (DeVlaming et al. 1982), GSI ratios, prior histological examination, and recent temporal larval density patterns all coincide, suggesting that the spawning periodicity illustrated by the GSI values were indeed valid in black croaker.

Gillnet samples were dominated by those from the 1997 year class, with additional strong representatives from the 1996 and 1998 year classes. Mortality-adjusted recruitment did not significantly correlate to mean summer sea surface temperatures, however, it does indicate that 1996–98 were peak recruitment years, along with 1994 and 1982 (fig. 11). These peaks were consistent with higher-than-normal sea surface temperatures brought about by El Niño Southern Oscillation events. That recruitment was significantly inversely correlated with total giant kelp (*Macrocystis pyrifera*) canopy area along the Palos Verdes Peninsula from 1982–2001 further suggests that recruitment is associated with warm waters. Although the direct cause of this relationship is unknown, the kelp area relationship may represent the larger-scale oceanographic conditions in the area. Principal among these may have been increased water temperature, which may have shortened the larval stage duration, thereby reducing overall larval mortality (Houde 1996; O'Connor et al. 2007). While black croaker has been consistently included in kelp bed/rocky reef assemblages, the loss of kelp coverage does not appear to directly affect their recruitment potential. Limbaugh (1961) and Stephens et al. (2006) both defined black croaker as associated with the rocky habitat and not among the kelp canopy/stipes. Impingement surveys recorded similar patterns, with Age-I, or younger, individuals peaking in 1997, and other smaller peaks in 1984 and 1993–94. Both the hindcasted recruitment and impingement results noted relatively low recruitment in cold-water, or La Niña, years such as 1999.

A strong, but statistically insignificant relationship was detected between chlorophyll-*a* concentrations and YOY impingement abundance, suggesting that some periods of higher primary productivity corresponded to increased recruitment rates. Lasker (1981) initially addressed this issue and found that while primary productivity may be elevated, the planktonic species contributing to the bulk of the productivity was as important as the level of productivity to recruitment rates. He found that high concentrations of nutrient-poor organisms, such as the dinoflagellate (*Gonyaulax polyhedra*), failed to support larval growth and led to poor recruitment. However, insufficient localized data on the phytoplankton and zooplankton communities were available to fully evaluate this hypothesis.

In conclusion, this research indicates that black croaker are relatively long lived in relation to other local sciaenids and do not exhibit a differential growth rate based on sex. Furthermore, a relatively robust population occurs near rocky headlands along the coast, such as the Palos Verdes Peninsula, and has wide-ranging interannual variability in population levels, presumably controlled by recruitment patterns. These recruitment patterns are controlled by a complex set of unknown biological and oceanographic features, although water temperature appears to be a significant factor.

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FEEDING HABITS OF THE BIGEYE THRESHER SHARK (*ALOPIAS SUPERCILIOSUS*) SAMPLED FROM THE CALIFORNIA-BASED DRIFT GILLNET FISHERY

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ABSTRACT

The diet of the bigeye thresher shark (*Alopias superciliosus*) was investigated by quantifying the stomach contents of sharks taken in the California-based drift gillnet fishery. Fishery observers collected stomachs of sharks ranging in size from 147 to 230 cm fork length during the 1998–99 and 2002–06 seasons in pelagic waters between the U.S.-Mexico border and Cape Mendocino, California. The frequency of prey items in stomachs by weight, number, and occurrence was determined and used to calculate two indices of dietary preference: the geometric index of importance (GII) and index of relative importance (IRI). Of 26 stomachs examined, 23 contained food items representing 20 taxa, indicating a broad trophic spectrum. Overall, the two indices consistently ranked the relative importance of prey items. Of the 10 taxa of teleosts found in the diet, fish of the family barracudinas (Paralepididae) represented the most important prey item (GII = 52.8; %IRI = 45.98), followed by Pacific hake (*Merluccius productus*; GII = 38.4; %IRI = 24.23), Pacific saury (*Cololabis saira*; GII = 22.2; %IRI = 8.08), Pacific mackerel (*Scomber japonicus*; GII = 17.3; %IRI = 3.92), and northern anchovy (*Engraulis mordax*; GII = 16.0; %IRI = 3.93). Of the eight taxa of cephalopods, jumbo squid (*Dosidicus gigas*; GII = 15.5; %IRI =3.61) and *Gonatus* spp. squid (GII = 11.0; %IRI = 0.63) were proportionately highest in ranking. The remaining two taxa were both crustaceans. Despite a sample size inadequate for characterizing the full breadth of the bigeye thresher diet, these data demonstrate that bigeye thresher sharks have a diverse diet and may feed opportunistically on locally and temporally available prey, including epipelagic, mesopelagic, epi-benthic, and deep-scattering-layer species. These data are consistent with fishery and electronic tracking data which demonstrate that the bigeye thresher shark is predominately a deep-water species, but spends time both within the deep-scattering and the mixed-surface layers.

INTRODUCTION

The bigeye thresher shark (*Alopias superciliosus*) occurs in tropical and temperate seas world-wide (Compagno 2001). An epipelagic and mesopelagic species, it is found primarily in oceanic and neritic waters, over continental and insular shelves where surface temperatures range from 15°–26°C (Gruber and Compagno 1981; Compagno 2001). Within the U.S. West Coast Exclusive Economic Zone (EEZ) it is commonly taken in the drift gillnet fishery that targets swordfish and has been caught from the U.S.-Mexico border to 45°N latitude. Bigeye thresher shark co-occurs in the drift gillnet catch with the common thresher shark (*Alopias vulpinus*) but is generally taken in offshore waters, whereas the common thresher is predominately found in near-shore waters. Annual U.S. West Coast landings of bigeye thresher sharks have averaged 26 mt since 1981 (range: 0 to 96 mt), with most animals taken between August and November (Hanan et al. 1993). In the Hawaii-based longline fisheries for swordfish and tunas, the bigeye thresher is the second most common shark encountered with relatively greater numbers caught in the deeper tuna sets (C. Boggs and W. Walsh, NOAA Pacific Islands Regional Observer Program, pers. comm.). Although they appear to have a broad geographic range, little is known of their migratory behavior and stock structure.

The vertical behavior of bigeye thresher sharks in the Pacific Ocean has been studied using electronic tags (Nakano et al. 2003; Musyl et al. 2004; Weng and Block 2004). Although only a few animals were tagged in these studies, they demonstrated distinct crepuscular vertical migrations, descending near sunrise and ascending near sunset. During the day, sharks were typically at depths between 200–550 m in 6°–12°C water and then shifted to shallower depths (10–130 m) and warmer waters (15°–26°C) at night. Their vertical behavior was similar to that of the megamouth shark, *Megachasma pelagios* (Nelson et al. 1997) and swordfish, *Xiphias gladius* (Carey and Robison 1981), both of which are believed to forage within the deep scattering layer (DSL).

Feeding behavior of bigeye thresher sharks is likely linked to a suite of unique morphological characteristics. Like the other thresher sharks, the bigeye thresher has a long caudal fin with which it seems to stun its prey; individuals are often tail-hooked when taken on longlines (Springer 1961; Compagno 2001). Unlike the other threshers, the large eyes of the bigeye thresher extend

onto the dorsal surface of the head, suggesting binocular vision both forward and overhead, which would enable foraging from below (Compagno 2001). Finally, the presence of a cranial rete mirabile indicates a mechanism for heat conservation and cranial endothermy (Carey and Teal 1969; Carey et al. 1971; Carey 1982; Block and Carey 1985; Weng and Block 2004). Elevated eye temperatures have been found to enhance foraging in cold waters by improving visual acuity (Fritsches et al. 2005).

Despite interest in their foraging ecology and their relatively common occurrence in a number of fisheries, little is known about the feeding habits of the bigeye thresher. Several studies report on stomach contents of bigeye threshers, but many of these describe only one or a few specimens (Fitch and Craig 1964; Bass et al. 1975; Stillwell and Casey 1976; Gruber and Compagno 1981; Polo-Silva et al. 2007). In addition, only one individual from all of these studies was from the northeast Pacific Ocean (Fitch and Craig 1964), where bigeye threshers are taken in longline fisheries on the high seas and in drift- and set-net fisheries closer to shore. This study reports on the foraging ecology of bigeye threshers caught in the pelagic drift gillnet swordfish fishery off the California coast based on their stomach contents.

METHODS

Stomachs of bigeye thresher sharks were collected during the 1998–99 and 2002–06 fishing seasons by NOAA Fisheries observers aboard commercial drift gillnet vessels. The drift gillnet fishery operates from 15 August to 31 January in U.S. federal waters from the U.S.-Mexico border to the Washington-Oregon state border. The majority of the fishery currently operates in the Southern California Bight (SCB). All vessels are required to fish with large mesh drift gillnets (≥14 in. stretched mesh) that are set overnight and retrieved in the morning. The nets are typically between 50 to 75 m deep and are set 12 m below the surface. The date, time, location, water temperature, characteristics of the net, fork length, and sex were recorded for each specimen. Stomachs were removed, frozen onboard, and later transferred to the Southwest Fisheries Science Center where they were processed within 6 months.

Stomach contents were sorted, digestive states noted, and prey were analyzed to the lowest possible taxon following the methods of Preti et al. (2001) and using keys when necessary to identify species from hard parts (Clothier 1950; Iverson and Pinkas 1970). Data were pooled across all years and analyzed by prey taxa for relative measures of prey quantities (RMPQs) as follows: percent occurrence by number (%N), percent frequency-of-occurrence (%F), and percent occurrence by weight (%W) of prey items. Weight was the actual weight of the prey remains, not the estimated weight of prey at ingestion. The value %N is the number of individuals of a specific taxon found in all stomachs divided by the total number of all prey found multiplied by 100; %F is the number of stomachs containing prey of a specific taxon divided by the total number of stomachs containing prey multiplied by 100; %W is the total weight of all remains of a specific taxon divided by the total weight of all prey remains found multiplied by 100 (Hyslop 1980; Preti et al. 2001). Empty stomachs, slurry, and detritus were not used when calculating percentages. The values listed above were used to calculate the three-dimensional dietary indices: the geometric index of importance (GII) and the index of relative importance (IRI).

The GII (Assis 1996; Mohan and Sankaran 1988; Fernández and Oyarzun 2001) and the IRI (Pinkas et al. 1971) were used to rank prey and to graphically represent the relative measures of prey quantity. We used each method to examine only the relative difference in ranking of prey types, because individual index values are not directly comparable.

The GII, in its generalized form, is calculated as:

$$GII_j = \frac{\left(\sum_{i=1}^{n} V_i \right)_j}{\sqrt{n}}, \quad (1)$$

where GII_j = index value for the j-th prey category, V_i = the magnitude of the vector for the i-th RMPQ of the j-th prey category, and n = the number of RMPQs used in the analysis. In our study this is expressed as:

$$GII_j = (\%N_j + \%W_j + \%F_j)/\sqrt{3} \quad (2)$$

The IRI for the j-th prey category is calculated as:

$$IRI_j = (\%N_j + \%W_j) * \%F_j \, . \quad (3)$$

The IRI value was converted to a percentage in order to facilitate comparisons among studies (Cortés 1997). Because the GII is a general form which can be used with any number of different types of RMPQs (Assis 1996), comparisons among studies is not always possible. Furthermore, %GII, which is the geometric mean of the RMPQs used and differs from GII by a single factor, does not necessarily sum to 100 when each individual RMPQ does not sum to 100. Therefore, we chose not to convert GII values to percentages as they would have had no added value, but they can easily be calculated from the data provided.

Randomized cumulative prey curves were constructed to examine trophic diversity and determine if sample size was sufficient to describe the full diet (Hurtubia 1973; Ferry and Cailliet 1996; Ferry et al. 1997; Gelsleichter et al. 1999; Yamaguchi and Taniuchi 2000). For this analysis, the order in which stomach contents were analyzed

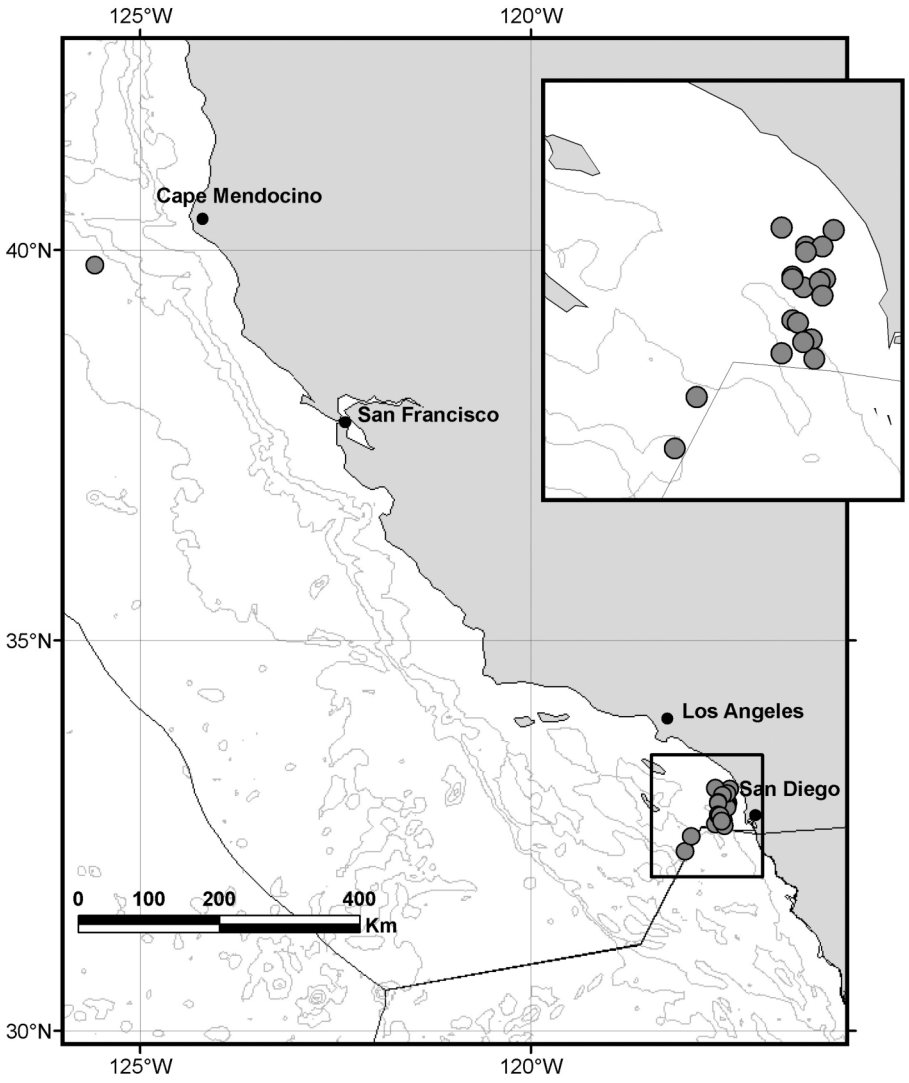

Figure 1. Collection locations for bigeye thresher shark (*Alopias superciliosus*) stomach samples, 1998–2006.

was randomized 10 times and the mean and standard error of the number of new prey observed was plotted for each consecutive stomach. A curve approaching an asymptote with low variability indicates that the number of stomachs examined was sufficient to characterize the diet.

RESULTS

Over the course of the study, 26 stomachs were collected during 18 observed trips. Most stomachs (18) were collected during the 2005 fishing season; two were collected during each of the 1999 and 2006 seasons, and one stomach from each of the 1998, 2002, 2003, and 2004 seasons. One shark was sampled in 1998 offshore of Cape Mendocino, California, and the rest were sampled in the SCB within 185 km of San Diego (fig. 1). Bottom depths ranged from 475 to 3327 m. Water temperature ranged from 16.0° to 21.1°C. Fishing depth of the nets in which the sharks were caught ranged from 11 m down to roughly 100 m, although the observers did not note where in the net the sharks were caught. The sharks ranged in size from 147 cm to 230 cm fork length (FL). Eight sharks were female, 17 male, and one was of unknown sex (fig. 2). Based on maturity studies of bigeye threshers in the western Pacific Ocean (Chen et al. 1997; Liu et al. 1998), nine of the males sampled were reproductively mature and all others sampled were subadults.

Of the 26 stomachs examined, 23 contained food representing a total of 20 taxa (tab. 1). Seventy-eight percent of the food items were in an advanced state of digestion; they were identified either by body parts that could not be reconstructed into measurable prey, hard parts only, or nearly digested remains. Consequently, in

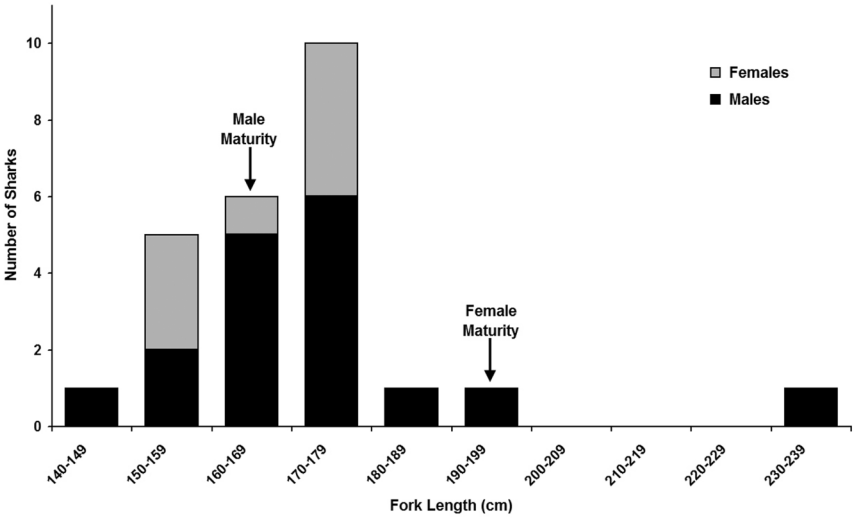

Figure 2. Length-frequency distribution of bigeye thresher sharks (*Alopias superciliosus*) sampled in the diet study. *N*=25 sharks; fork length and sex were not determined for one of the 26 sharks in the study.

TABLE 1
Quantitative prey composition of the bigeye thresher shark (*Alopias superciliosus*) along the California Coast. A total of 23 stomachs containing food and three without food were examined. Prey items are shown by decreasing values of GII. See methods for descriptions of the measured values.

Prey species	*W (g)*	*%W*	*N*	*%N*	*F*	*%F*	GII	IRI	%IRI
Barracudinas, Paralepididae	2076.9	21.62	69	26.34	10	43.48	52.79	2084.96	45.98
Pacific hake, *Merluccius productus*	1378.4	14.35	57	21.76	7	30.43	38.42	1098.80	24.23
Pacific saury, *Cololabis saira*	631.6	6.57	38	14.50	4	17.39	22.21	366.57	8.08
Pacific mackerel, *Scomber japonicus*	383.3	3.99	11	4.20	5	21.74	17.28	178.00	3.93
Northern anchovy, *Engraulis mordax*	141.8	1.48	23	8.78	4	17.39	15.96	178.34	3.93
Unidentified Teleostei	125.0	1.30	22	8.40	4	17.39	15.64	168.66	3.72
Jumbo squid, *Dosidicus gigas*	282.1	2.94	17	6.49	4	17.39	15.48	163.91	3.62
Jack mackerel, *Trachurus symmetricus*	1576.0	16.40	3	1.15	1	4.35	12.64	76.30	1.68
King-of-the-salmon, *Trachipterus altivelis*	1503.7	15.65	3	1.15	1	4.35	12.21	73.03	1.61
Bocaccio rockfish, *Sebastes paucispinis*	1404.4	14.62	1	0.38	1	4.35	11.17	65.22	1.44
Gonatus spp.	10.5	0.11	4	1.53	4	17.39	10.99	28.46	0.63
Flowervase jewell squid, *Histioteuthis dofleini*	23.3	0.24	3	1.15	3	13.04	8.33	18.10	0.40
Unidentified Teuthoidea	40.8	0.42	2	0.76	2	8.70	5.71	10.33	0.23
Market squid, *Loligo opalescens*	21.8	0.23	2	0.76	2	8.70	5.59	8.61	0.19
Pacific sardine, *Sardinops sagax*	5.5	0.06	2	0.76	2	8.70	5.49	7.14	0.16
Unidentified Crustacea	2.0	0.02	1	0.38	1	4.35	2.74	1.75	0.04
Boreopacific gonate squid, *Gonatopsis borealis*	0.01	0.00	1	0.38	1	4.35	2.73	1.66	0.04
Octopoteuthis sp.	0.01	0.00	1	0.38	1	4.35	2.73	1.66	0.04
Cranchia, *Cranchia scabra*	0.01	0.00	1	0.38	1	4.35	2.73	1.66	0.04
Pelagic red crab, *Pleuroncodes planipes*	0.01	0.00	1	0.38	1	4.35	2.73	1.66	0.04

some cases, for example for *Gonatus* spp. squid, the ranking of the relative indices of importance may be lower than for other prey found intact, but in fewer stomachs. Table 1 lists each of the RMPQs for all prey found, as well as the calculated three-dimensional relative indices of importance. RMPQs for the most important prey taxa, as determined by the highest GII and %IRI rankings or the frequency of occurrence in four or more stomachs, is also shown graphically (fig. 3).

Rankings based on GII and IRI were nearly identical (tab. 1). Teleosts of the family barracudinas (Paralepididae) were the most important prey item in number, frequency, weight, and based on the combined indices. Almost half of the barracudinas remains (44%) were identified as duckbill barracudina (*Magnisudis atlantica*) using otoliths. Other dominant teleost prey included Pacific hake (*Merluccius productus*), Pacific saury (*Cololabis saira*), Pacific mackerel (*Scomber japonicus*), and northern anchovy (*Engraulis mordax*). King-of-the-salmon (*Trachipterus altivelis*) was only found in the shark caught farthest north, off Cape Mendocino, California. Eight taxa of cephalopods were also found with jumbo squid (*Dosidicus gigas*) and Gonatus spp. squid making the greatest contributions to the diet. One unidentified crustacean and remains of

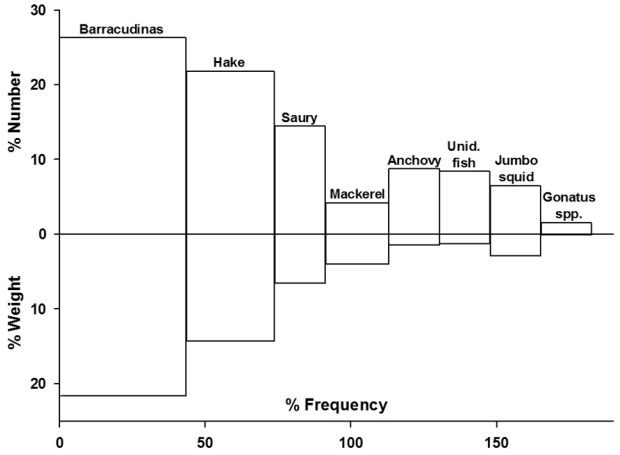

Figure 3. Graphical representation of bigeye thresher shark (*Alopias superciliosus*) diet using RMPQ values % weight, % frequency of occurrence, and % number for the major prey items.

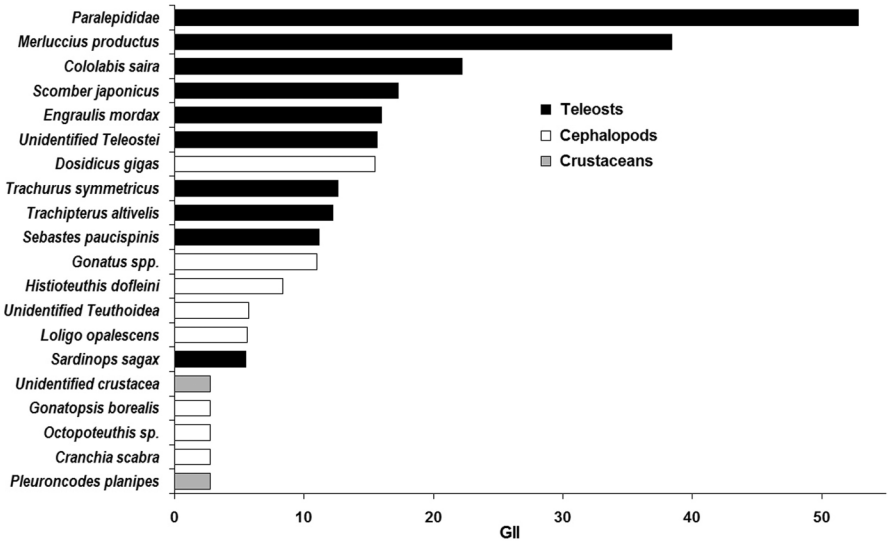

Figure 4. Results of geometric index of importance (GII) analyses for the 20 prey taxa (*N* = 23 stomachs containing prey).

a pelagic red crab (*Pleuroncodes planipes*) were also found (tab. 1; fig. 4).

Cumulative prey curves described a generally increasing relationship that did not reach full asymptotic stabilization (fig. 5). Thus, our sample size may not have been sufficient to describe the overall trophic diversity of this species' diet. Given the low sample size, further subdivision of the samples by year, sex, or size class would not have been appropriate to examine interannual, sex-specific, or ontogenetic differences in diets for this species.

DISCUSSION

General Findings and Study Limitations

This is the first study to report on the diet of the bigeye thresher shark in the U.S. West Coast EEZ with the exception of an early report including only one animal (Fitch and Craig 1964). Results suggest that bigeye thresher sharks are opportunistic feeders, foraging on diverse species covering a broad range of habitats. Overall, 20 species of prey occurred in only 23 stomachs. The prey identified included fish, cephalopods, and crustaceans from a range of habitats. The species making up the greatest component of the bigeye thresher shark diet in southern California were mesopelagic and epipelagic teleosts and are listed in order of importance: barracudinas, Pacific hake, Pacific saury, Pacific mackerel, and northern anchovy. At least eight cephalopod species were also observed, although most species were found in only a few stomachs. Of the cephalopods, the jumbo squid, which has shown up in large numbers off the California coast in recent years (Field et al. 2007), was the highest ranked

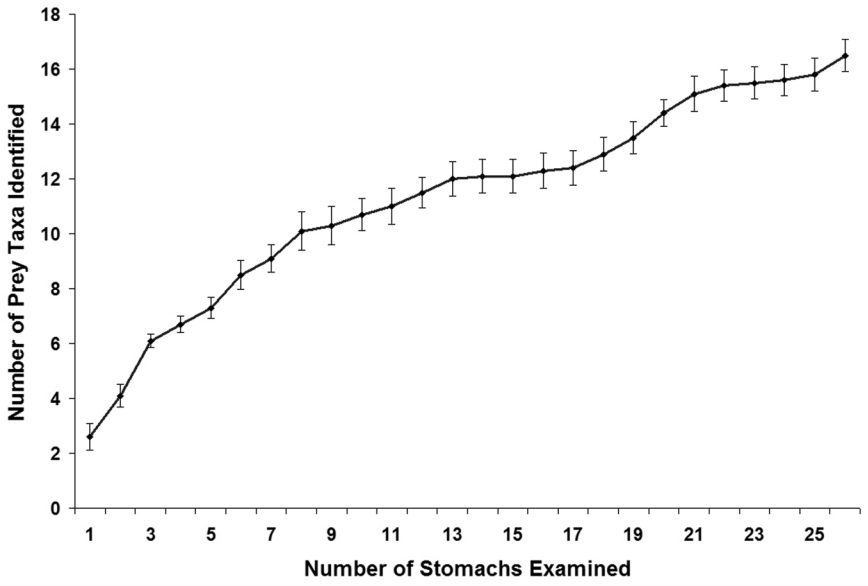

Figure 5. Randomized cumulative prey curve for the bigeye thresher shark (*Alopias superciliosus*) diet sample. Mean values are plotted; error bars represent ± SE (*N* = 26 stomachs examined). The curve has not reached an asymptote and the error bars are not declining indicating that the sample size may be insufficient to fully describe the diet.

species. Squid from the genus *Gonatus* were also important. Crustaceans appear not to be highly important in the SCB over the sampling season; only two taxa were found, each in only one stomach.

Although this study provides some of the first insights into the foraging ecology and biology of bigeye thresher sharks off the California coast, we caution that the sample size may have been insufficient to fully characterize the bigeye thresher diet in this area. Even more novel prey would have likely been encountered as sample size increased, as indicated by the mean cumulative prey curve. Also, because most of the samples were collected in a single season, interannual comparisons were not possible, nor were examinations of ontogenetic or sex-specific differences in foraging ecology. Continued sampling is ongoing in order to address these limitations.

Sampling sufficient numbers of bigeye thresher sharks off the California coast is difficult given that the encounter rates are relatively low in this fishery and only 20% of the trips are observed. Sampling effort for this study has been variable. Prior to the 2005 season, observers only casually collected bigeye thresher stomachs. In 2004, bigeye threshers became a federally managed species under the Pacific Fishery Management Council's Fishery Management Plan for Highly Migratory Species, and consequently NOAA Fisheries asked observers to prioritize collecting bigeye thresher stomachs in order to learn more about their biology and ecology. Even with increased priority placed on collecting bigeye thresher samples, few specimens were collected in 2006, suggesting that differences in availability may have affected our sample sizes. We examined the nominal catch-per-unit-effort (nCPUE) of bigeye threshers in the observed catch of the drift gillnet fishery over the study period (unpublished data; NOAA Southwest Region Fishery Observer Program). Nominal CPUE was highest at 0.33 sharks per set during the 2005 season. Oceanographic conditions could be one factor responsible for variations in bigeye thresher catch rates. We looked at both the El Niño Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) indices (http://cses.washington.edu/cig/pnwc/compensopdo.shtml; http://www.cdc.noaa.gov/people/klaus.wolter/MEI/) to determine whether El Niño, La Niña, or decadal regimes affected catch rates during the study period. There were mild El Niño conditions during fishing seasons 2002, 2004, and 2006, and La Niña conditions during 1998, 1999, and 2005. More significantly, there was a regime shift during the sampling period; 1999–2002 was a cool regime and 2003–05 was a warm regime based on the PDO index. Nominal CPUE was nearly an order of magnitude higher during the PDO warm phase (2003–06: nCPUE = 0.17 ± 0.10 sharks per set) than during the cool phase (1999–2002: nCPUE = 0.02 ± 0.003 sharks per set). But the ENSO index itself does not seem correlated with nCPUE, at least over the last decade. The three seasons with the highest nCPUE (2005, 2006, and 2003) are classified respectively as La Niña, El Niño, and neutral based on the ENSO index. Alternatively, the four seasons with the lowest nCPUE (2002, 1999, 2000, and 2001) are classified respectively as El Niño, two La Niñas, and neutral.

While the three-dimensional diet indices consistently ranked the top species, the use of these standard indices may misrepresent the importance of some prey. Each

RMPQ measures a different aspect of the diet (bulk versus number versus occurrence, in the case of the present study) and it has long been emphasized that each has its limitations and biases toward different aspects of the diet (Hyslop 1980; Cortés 1997). Furthermore, even the three-dimensional indices may alter conclusions about the importance of prey taxa when taxa are combined into generalized groups (Hansson 1998). We provide tables and analyses with the highest prey resolution possible allowing readers to calculate alternate indices of their choice.

We were not able to overcome the fact that indices may underrepresent prey identified by beaks or otoliths alone as a consequence of various stages of digestion in the stomachs. Unfortunately, the quantitative relationships between hard-part size and mass that would be necessary to calculate weight at ingestion are not available for all of the prey species.

A final aspect which limits conclusions about bigeye thresher foraging ecology is the lack of information on when and where feeding occurs. There are currently no data available about what time of day bigeye thresher sharks actually consume prey. Although the fishery in which the sharks were caught for the current study operates at night and fishes from roughly 12 m to 90 m deep, prey in advanced states of digestion as well as some fresh prey were found in the stomachs examined. Without information on how rapid digestion occurs and at what time and depth the fish were actually caught, it is not possible to further discern a precise measure of the time and depth of foraging.

Despite these limitations, these data comprise the most comprehensive study to date of the foraging ecology of bigeye threshers off the California coast.

Intraspecies Comparisons Among Areas

The results of this study demonstrate considerable overlap with other studies of bigeye thresher shark diets. Although many of the prey species differ, the most important items at most locations appear to be epipelagic and mesopelagic fish and squid. The only prior report on bigeye thresher diets in the North Pacific Ocean reported six Pacific hake (*Merluccius productus*) in the stomach of one specimen taken off California (Fitch and Craig 1964). In the present study, Pacific hake was the second most important prey. There are a number of interesting differences in the species composition observed both across and within ocean basins; while a small istiophorid was reported in one of 18 stomachs in the Atlantic Ocean (Stillwell and Casey 1976), none have yet been observed in the northeast Pacific Ocean (Fitch and Craig 1964; current study). It should be noted, however, that small istiophorids are not common in the area from which these samples were collected. The Atlantic study also reported that scombrids accounted for the greatest amount of fish remains (27%), whereas in this study Pacific mackerel was present in only five stomachs and was less important than barracudinas, hake, and saury. Also, no elasmobranchs were found in the current study, although they occurred in the diet of a bigeye thresher off South Africa (Bass et al. 1975). Comparing the results from the SCB to Ecuador (Polo-Silva et al. 2007), where the only comprehensive study of bigeye thresher diets, in which each prey species was enumerated, has been conducted, mesopelagic and epipelagic fish and cephalopods were important in both areas. The most important prey species in the Ecuador study were silver drum (*Larimus argenteus*), south Pacific hake (*Merluccius gayi*), jumbo squid (*Dosidicus gigas*), and lamp fish (*Benthosema panamense*). A larger number of epi-benthic and reef-associated species were also found, presumably due to the habitat fished; the fishery sampled was a coastal artisanal fishery unlike the pelagic fishery sampled here. As in the present study, the number of prey species found was relatively high; the 107 bigeye thresher stomachs containing prey had a minimum of 27 different species in their stomachs.

Comparisons with Sympatric Species

The bigeye thresher shark co-occurs with the common thresher, shortfin mako (*Isurus oxyrinchus*), and blue shark (*Prionace glauca*) in the catch of the California drift gillnet fishery. A comparison of the bigeye thresher shark diet to that of other overlapping pelagic sharks demonstrates variability in both the number and types of species encountered in the diets.

Those species for which published diet information is available from California waters include the common thresher shark (Preti et al. 2001; Preti et al. 2004) and blue shark (Tricas 1979; Harvey 1989). Combined, the common thresher shark studies reported 21 prey taxa in 174 stomachs containing food; however, the diet was more diverse (20 taxa) during a warm-water year following El Niño (Preti et al. 2001) than during a more typical year (eight taxa; Preti et al. 2004). In both cases, the most important prey were epipelagic species such as northern anchovy, Pacific hake, Pacific sardine, Pacific mackerel, and market squid (*Loligo opalescens*). The two blue shark studies combined reported 37 prey taxa (identified at least to genera) in a total of 226 stomachs; prey included primarily fish, cephalopods, and crustaceans (Tricas 1979; Harvey 1989). While there were considerable differences in the species composition (13 taxa overlapped), the prey covered the same range of habitats including a number of epi-benthic species (spiny dogfish and rockfish), teleosts from the epipelagic zone (anchovy, herring, and jack mackerel), and fish and squid associated with the DSL (myctophids, *Dosidicus* and *Histioteuthis*). Based both on electronic tagging studies and the diet composition, the blue shark likely forages

on DSL-associated species both at night near the surface as well as during the day at depth (Harvey 1989; Carey and Scharold 1990).

Comparison of bigeye thresher, common thresher, and shortfin mako sharks' diets for a single season (2005–06) revealed the most prey taxa in the bigeye thresher sample, despite a smaller sample size (bigeye thresher: 14 prey taxa in 15 stomachs; mako shark: 11 prey taxa in 32 stomachs; common thresher: five prey taxa in 41 stomachs; Southwest Fisheries Science Center unpubl. results). The bigeye thresher appears to forage across habitats whereas more niche separation is apparent for the other species. The stomach contents of the common thresher were dominated by epipelagic species. Shortfin mako stomachs contained a large variety of taxa, including epipelagic and mesopelagic teleosts and cephalopods, but no epi-benthic species.

Swordfish, another obvious overlapping large pelagic species, is the target of the drift gillnet fishery. Based on electronic tagging studies in a few areas, the bigeye thresher demonstrates the same general diel vertical migration as swordfish (Carey and Robison 1981; Carey 1990; Nakano et al. 2003; Musyl et al. 2004; Weng and Block 2004). Swordfish also forage on many of the same prey (Mearns et al. 1981; Moteki et al. 2001; Markaida and Hochberg 2005); swordfish taken by drift gillnets in the SCB were found to feed predominately on northern anchovy (%IRI = 42.6) and Pacific hake (%IRI = 41.9; Mearns et al. 1981), both of which were identified in the top five prey for bigeye threshers in this study.

Ecology of the Main Prey Taxa

To further explore the foraging ecology of the bigeye thresher sharks, we considered the habitats and behaviors of the top prey species. Given the limitations associated with the RMPQs and indices, we examined the characteristics of the seven taxa that fell into the top 11 prey species for both the GII and %IRI and that were found in a minimum of four stomachs. These prey taxa include barracudinas, Pacific hake, Pacific saury, Pacific mackerel, northern anchovy, jumbo squid, and *Gonatus* spp. squid.

Based on the biology of the seven top taxa, it seems that bigeye thresher sharks forage across a range of habitats. A number of the more important prey species are found in or associated with the DSL, including barracudinas, jumbo squid, and *Gonatus* spp. squids (Anderson 1977; Magnússon 1996; Markaida and Sosa 2003; Gilly et al. 2006). That bigeye threshers feed within the DSL is consistent with the findings of the other diet studies and has been deduced based on their vertical migratory behavior. Although none of the tracking studies have been conducted within the SCB or California Current, electronic tagging data show a diel migration that seems to parallel the migration of the DSL (Nakano et al. 2003; Musyl et al. 2004; Weng and Block 2004). In addition to foraging within the DSL, bigeye thresher sharks also appear to forage near the top of the water column. Pacific saury, Pacific mackerel, and northern anchovy are epipelagic, remaining largely in the surface-mixed layer (Jacobson 1992; Kato 1992; Konno and Wolf 1992). The final species of the top seven taxa (Pacific hake) has been characterized both as demersal and pelagic. When found over the continental shelf, it remains associated with the bottom during the day but forages in surface waters at night (Alverson and Larkins 1969; Quirollo 1992). The occurrence of this species suggests the possibility that the bigeye thresher also feeds near the benthos, similar to swordfish that feed on banks in near-shore waters (Carey and Robison 1981; Carey 1990). Finally, the presence of bocaccio, although only in one stomach, confirms the potential for epi-benthic foraging because this species seldom moves more than 10 m above the bottom (Starr et al. 2002). These behaviors are similar to those of sharks off Ecuador that also fed on epi-benthic species. The bigeye thresher is capable of foraging throughout the water column from the surface to the DSL as well as on demersal or reef-associated species.

In the SCB, the relative abundance of some of the top teleost prey species is known through larval collections taken during the annual CalCOFI cruises. Based on several egg production models, we know that larval abundance is representative of the abundance of breeding adults (Lasker 1985; Ralston et al. 2003). The standardized larval abundances of the five most important teleost prey in the bigeye thresher diet were examined in order to get an idea of whether bigeye threshers are feeding on abundant prey or specifically seeking prey that are less abundant in the SCB. While the larval counts may not reliably indicate prey that are neither spawning during the surveys nor vulnerable to the sampling gear, these counts nonetheless provide some information on the presence of the prey in the SCB. The relative ranking of larval abundances for the top teleost prey are: Barracudinas spp. – 43, 69, and 96 for three taxa identified, none of which were the duckbill barracudinas; Pacific hake – 2; Pacific saury – 81; Pacific mackerel – 21; and northern anchovy – 1 (Moser et al. 2001). Thus, the bigeye thresher diet includes the two most abundant species as well as some less abundant species. As for the cephalopod prey, recent evidence indicates that jumbo squid have been increasing in abundance throughout the California Current since 1998 (Field et al. 2007; Zeidberg and Robison 2007). It is interesting to note that the jumbo squid was not found in samples collected prior to the fall of 2005 in the present study. *Gonatus* spp. squid are the most abundant squids in the subarctic Pacific Ocean, and several species are found regularly in the California

Current waters (Anderson 1977; Okutani et al. 1988; Hunt and Seibel 2000). Without identification to the species level, however, it is not possible to know the relative abundance of those consumed by bigeye threshers in the current study.

Based on the ecology of the top prey species, it appears that many, but not all, are schooling prey. Jumbo squid, bocaccio, and king-of-the-salmon, for example, are not likely to be found in cohesive schools that are typical of anchovy and mackerel. In addition, studies in other areas demonstrated that bigeye threshers occasionally feed on benthic prey. Reportedly, thresher sharks use their long tail to stun schooling prey while foraging (Springer 1961; Compagno 2001); however, whether the tail is used to forage in all habitats is not known given that some prey may be more solitary, demersal, or reef-associated.

As previously mentioned, one aspect which limits conclusions about bigeye thresher shark foraging ecology is the lack of information on when feeding occurs. Despite suggestions that they are primarily a nocturnal species (Nakano et al. 2003), it is more likely that bigeye threshers forage both during the day and the night. During the day, their vertical range overlaps with the DSL-associated organisms found in their stomachs, and their large eyes and cranial endothermy are ideal for foraging in dark, cold waters (Block and Carey 1985; Musyl et al. 2004; Weng and Block 2004; Fritsches et al. 2005). Swordfish, which are known to forage at depth during the day, have similar adaptations (Carey et al. 1971; Carey and Robison 1981; Carey 1990; Fritsches et al. 2005). Also, the diel vertical movements are extensive and it seems unlikely that these would be undertaken solely to avoid predation, given their large size and trophic position.

Conclusions

The bigeye thresher shark appears to be more of a generalist and opportunist than the other pelagic sharks of the SCB, with the possible exception of the blue shark. A broad range of prey from mesopelagic, epipelagic, and epi-benthic habitats was observed in the stomachs of only 23 individuals. While this study provides the most detailed information on the diet of bigeye thresher sharks in the north Pacific Ocean, additional work remains. No electronic tagging studies of bigeye threshers have been conducted in the SCB. It would be of great interest to examine the vertical movement patterns for the same region where stomachs are collected. Also, conclusions about the relative importance of different prey items could be improved by estimating the weight of the ingested prey. Finally, because bigeye threshers are relatively rare in the drift gillnet fishery catch, the sample size in this study is small and covers a narrow temporal and spatial scope. If possible, a broader sampling regime would reduce uncertainty about patterns of foraging times and depths, and allow for an examination of interannual differences and the impacts of various environmental factors and location on diet. Nevertheless, the detailed information presented is critical as we move toward multispecies assessments and a better understanding of the interactions among this top predator and its prey within the California Current ecosystem.

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IDENTIFICATION, DESCRIPTION, AND DAILY GROWTH OF PELAGIC LARVAL AND JUVENILE SQUARESPOT ROCKFISH, *SEBASTES HOPKINSI* (FAMILY SEBASTIDAE)

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ABSTRACT

Identifying pelagic larval and juvenile *Sebastes* spp. is important for biomass estimates and recruitment studies. However, only about 50% of *Sebastes* spp. can be unambiguously identified. In this study, pelagic larval and juvenile squarespot rockfish (*Sebastes hopkinsi*) are described and a series of fish ranging from 3.5 mm notochord length to 52.3 mm standard length are illustrated. Species descriptions include pigmentation patterns, meristic characters, morphometric measurements, head spination, and otolith morphology. Species identification was confirmed using mitochondrial DNA sequence data. The growth rate for small larvae averaged 0.17 mm/day, while for late larvae and juveniles the average growth rate increased to 0.47 mm/day; both of these growth rates are typical for early life stages of *Sebastes* from California.

INTRODUCTION

Accurate identification of pelagic larval and juvenile *Sebastes* spp. is important for biomass estimates and recruitment studies (Hunter and Lo 1993; Ralston et al. 2003). Within the northeastern Pacific Ocean region, there are at least 72 species of rockfishes, *Sebastes s*pp. (Love et al. 2002). Differentiating them in the larval (and to a lesser extent the juvenile) stages is extremely difficult due to similar pigment patterns. Many species are even difficult to tell apart as adults (e.g., the subgenus *Sebastomus*). Complete descriptions of these early life stages exist for only 20 rockfishes; for 10 of these species only the juvenile stages are described, for seven species, only some larval stages are described; for the remainder we have few or no descriptions, and only a few images (see Laroche[1], Matarese et al. 1989; Moser 1996). Larval and juvenile *Sebastes* spp. have been identified through rearing studies and descriptions based on a size-series of field-caught specimens (Matarese et al. 1989; Moser 1996). Otolith characteristics have also proven useful in discerning some *Sebastes* spp. (Laidig and Ralston 1995), and genetic methods are another effective identification tool (Rocha-Olivares et al. 2000; Taylor et al. 2004; Pearse et al. 2007).

Sebastes spp. comprise a substantial portion of the groundfish fishery off the west coast of North America, although the abundances of several of these commercial species (e.g., canary rockfish, *S. pinniger*) have declined in recent years (PFMC 2004). With a decrease in abundance of large-sized rockfish, smaller-sized rockfish are appearing more frequently in landings. The small-sized squarespot rockfish (*Sebastes hopkinsi*; maximum size of 29 cm total length) is now the most commonly landed rockfish in the recreational catch from southern California (Love et al. 2002). *Sebastes hopkinsi* generally occur around rocky outcrops, boulder fields, and hard fractured substrata between 18–224 m depth. Although they may be solitary, *S. hopkinsi* are often found in large aggregations numbering in the thousands (Love et al. 2002). While *S. hopkinsi* has recreational value, it is also an ecologically important species, commonly found in the stomachs of pinnipeds (NMFS 1997).

In this study, we provide the means to identify the larvae and pelagic juveniles of *S. hopkinsi*, and also examine the age and growth from otoliths. We use mitochondrial DNA (mtDNA) sequence data to confirm the pelagic larval through juvenile *S. hopkinsi* specimens identified based on morphological, meristic, and pigmentation characters, and in order to assure that the assembled developmental series is monospecific.

METHODS

Specimen Collection

Specimens of pelagic larval and juvenile *S. hopkinsi* were obtained from research cruises aboard the NOAA RV *David Starr Jordan* off the coast of California. Preflexion, flexion, and postflexion larvae, up to 16.0 mm standard length (SL), were collected off southern California 1-15 April 1999 in oblique bongo net (0.505 mm mesh) tows through the upper 212 m of the water column during CalCOFI cruise 9904 and following standard CalCOFI procedures (Kramer et al. 1972). Sampling effort was distributed between CalCOFI lines 80 and 93, with larval *S. hopkinsi* collected at 19 of the 58 stations surveyed. Positive larval collections occurred at the more inshore stations of the survey (covering most of

[1]Laroche, W. A. 1987. Guide to larval and juvenile rockfishes (*Sebastes*) of North America. Box 216, Enosburg Falls, VT 05450. Unpubl. Manu. 311 pp.

the Southern California Bight). Samples from the starboard side of the bongo net were fixed in 5% sodium borate buffered formalin for later species identification, while those from the port side were fixed in 95% ethanol for use in molecular identification and larval aging studies. Late-stage larval and juvenile specimens were collected from central California from mid-May to mid-June during 1990–93 and 2001 and between Bodega Bay (north of San Francisco) and Cypress Point (south of Monterey Bay) using a modified Cobb midwater trawl with a 26 m headrope and a 9.5 mm stretched mesh codend liner. Specimens were frozen at sea for later analysis.

Meristics, Morphometrics, and Body Pigmentation

A total of 236 pelagic larval and juvenile *S. hopkinsi,* ranging in total length from 3.5 to 52.3 mm, were examined for pigmentation patterns and physical characteristics. Notochord length (NL) was measured on all flexion and preflexion larvae, and SL was measured for postflexion individuals. Counts of dorsal, anal, and pectoral fin rays, and the number of gill rakers on the first gill arch were recorded whenever possible, and subsequently used in identifications. Accurate gill raker counts were obtained only from fish larger than 15 mm SL. Specimens greater than 19.9 mm were identified using meristic characters (fin ray and gill raker counts) and head spination (Matarese et al. 1989; Moreland and Reilly 1991; Moser 1996; Laroche[1]), and pigment patterns were recorded.

Larval *S. hopkinsi* collected from the CalCOFI cruise (n = 85) were first identified to species genetically because they could not be identified through other means (fin ray and gill raker counts). Pigment patterns were recorded from these fish after positive genetic identifications. Due to the removal of tissue for genetic identification, complete pigment patterns for the caudal fin and peduncle could not be determined for each specimen.

Morphometric measurements recorded for 30 *S. hopkinsi*, ranging in size from 14.4–45.0 mm SL, included snout-to-anus length, head length, snout length, eye diameter, body depth at the pectoral fin base, body depth at anus, and pectoral fin length, and followed Richardson and Laroche's methods (1979). Head spination was examined on 22 specimens (6.0 to 45.0 mm SL) stained with Alizarin red S. Terminology for head spination follows Richardson and Laroche (1979).

Otolith Examination

Sagittal otoliths were removed from the rockfish and ages were obtained by increment counts beginning at the first growth increment after the extrusion check (a mark in the otolith that forms when the larva is initially released from the mother) using a compound microscope at 1000× magnification (Laidig et al. 1991). Growth increments were not validated during this study, and no other researchers have conducted validation studies on this species. However, these counts were assumed to correspond to daily ages because the formation of daily growth increments has been validated for other cooccurring rockfish species, including *S. jordani* (shortbelly rockfish) (Laidig et al. 1991), *S. paucispinis* (bocaccio), *S. goodei* (chilipepper), *S. entomelas* (widow rockfish), and *S. flavidus* (yellowtail rockfish) (Woodbury and Ralston 1991). The radius of each otolith was measured from the center to the postrostral edge of the extrusion check for comparison with similar measurements from other *Sebastes* spp. (Laidig and Ralston 1995). Transformation from the larval stage to the juvenile stage was ascertained by the occurrence of accessory growth primordia (Laidig et al. 1991). Accessory primordia are areas away from the otolith core from which new increment growth begins (also called secondary growth centers or primordia).

Molecular Identification

Genomic DNA was extracted from caudal fin, muscle, or eye tissue using a chelex extraction protocol (Walsh et al. 1991). The polymerase chain reaction (PCR) was used to amplify 862 bp of the mtDNA cytochrome-*b* gene in a 1× buffer containing 20 mM Tris-HCl, 50 mM KCl, 1.5 mM $MgCl_2$, 800 μM dNTPs, 0.3 μM of each primer, and 0.5 units *Taq* DNA polymerase (New England Biolabs). Primers included previously published GluRF and CB3RF (Rocha-Olivares et al. 1999) and internal custom primers (CB306F 5'-TTACTACGGCTCV-TACCT-3, Cb521R 5'-GTTGCATTGTCTACTGAG-3', and CB364F, 5'-CTAGTTATAATAACTGCTTT-3'). The PCR temperature profile was: 90°C for 2:00 min, followed by 36 cycles of denaturing at 92°C for 0:45 min, annealing at 50°C for 1:00 min, and elongation at 72°C for 1:30 min. PCR products were cleaned using either EXOSAP-IT (USB Corp.) or a Qiaquick PCR purification kit (Qiagen) and according to the manufacturer's protocol. Cleaned PCR products were cycle-sequenced using BigDye v.3.1 (Applied Biosystems) using internal sequencing primers and analyzed on an ABI 3100 automated capillary sequencer (Applied Biosystems). Chromatogram data for sequenced DNA were aligned using the biosequence analysis and editor program, Sequencher (v. 4.1.1 Gene Codes).

Sequences were compared to DNA reference sequence data of 374 independent haplotypes that represented 67 species of identified adult *Sebastes* using an iterative approach within the software program Phylogenetic Analysis Using Parsimony (PAUP* 4b10; Swofford 2000) or Molecular Evolutionary Genetic Analysis (MEGA v2.1; Kumar et al. 2001) with the optimality criterion set to distance (number of bp differences divided by total bp

sequenced). A complete listing of species included in the PAUP reference file is included in Taylor et al. (2004). Nonparametric bootstrapping was used (1000 replications, MAXTREES set to 1000) to cluster each unknown haplotype within a database of consensus haplotypes (consensus = most common haplotype from a database of up to 17 known adults) for putative identification. The identification of the specimen was accepted if it clustered with a single haplotype of a reference species with a bootstrap value of at least 90%. The distance between reference haplotypes and the unknown haplotype was examined to confirm that the unknown fell within the expected intra-specific diversity based on the reference data. A first identification was accepted if a specimen's sequence clustered with a single haplotype of a species with a bootstrap of less than 90%. Secondary analysis was performed using all available haplotypes of at least the three nearest (in distance) species to the unknown haplotype. The species of the unknown haplotype was identified by comparing it to the sequences of the reference species. Additionally, sequences were screened for unique single nucleotide polymorphisms that differentiate *S. hopkinsi* from all other *Sebastes* spp. in the eastern Pacific Ocean (J. Hyde unpublished data). Intra-specific diversity for reference species in the northeast Pacific Ocean has a mean distance of 0.006 with a minimum of 0.0 (e.g., *S. jordani*) and a maximum of 0.041 (in *S. hopkinsi*).

RESULTS

General Development

The smallest *S. hopkinsi* larva collected was 3.5 mm NL. Flexion began at approximately 6.0 mm NL and

TABLE 1
Frequency of occurrence of soft dorsal, anal, and pectoral fin ray counts, and gill raker counts from 181 *Sebastes hopkinsi*, squarespot rockfish. Gill raker counts are from specimens 15 mm SL and larger.

	Dorsal fin count				Anal fin count			Pectoral fin count			Gill raker count							
	13	14	15	16	6	7	8	16	17	18	34	35	36	37	38	39	40	41
Frequency of Occurrence	3	82	85	11	14	162	5	10	155	10	2	7	11	21	29	27	6	4
Percent Occurrence	2	45	47	6	7	90	3	6	88	6	2	6	10	20	27	25	6	4

TABLE 2
Morphometric measurements (in mm) from individuals of *Sebastes hopkinsi*, squarespot rockfish. Number in parentheses represents the ratio of the measurements to the SL.

SL	Snout-anus length	Head length	Snout length	Eye diameter	Body depth at pectoral base	Body depth at anus	Pectoral fin length
14.4	8.5 (.59)	5.0 (.35)	1.4 (1.0)	1.9 (.13)	3.6 (.25)	2.1 (.15)	N/A
14.8	8.9 (.60)	4.7 (.32)	1.5 (.10)	2.0 (.14)	3.8 (.26)	3.0 (.20)	2.4 (.16)
15.0	9.0 (.60)	5.1 (.34)	1.5 (.10)	1.6 (.11)	4.0 (.27)	3.3 (.22)	2.6 (.17)
15.1	9.3 (.62)	5.0 (.33)	1.4 (.09)	2.0 (.13)	3.8 (.25)	3.1 (.21)	2.8 (.19)
15.7	9.4 (.60)	5.0 (.32)	1.6 (.10)	2.2 (.14)	4.5 (.29)	3.4 (.22)	2.9 (.18)
16.1	9.5 (.59)	5.1 (.32)	1.6 (.10)	2.1 (.13)	4.2 (.26)	3.3 (.20)	2.4 (.15)
16.5	9.7 (.59)	5.9 (.36)	1.9 (.11)	2.2 (.13)	4.3 (.26)	3.4 (.21)	3.6 (.22)
16.7	10.2 (.61)	5.9 (.35)	1.9 (.11)	2.4 (.14)	4.2 (.25)	3.4 (.20)	3.5 (.21)
18.1	11.0 (.61)	6.3 (.35)	1.9 (.10)	2.4 (.13)	4.8 (.27)	4.1 (.23)	3.8 (.21)
18.4	10.9 (.59)	6.1 (.33)	1.7 (.09)	2.2 (.12)	5.0 (.27)	4.2 (.23)	3.7 (.20)
18.5	10.3 (.56)	5.9 (.32)	1.4 (.08)	2.1 (.11)	4.5 (.24)	4.1 (.22)	3.4 (.18)
19.4	11.4 (.59)	6.1 (.31)	1.7 (.09)	2.2 (.11)	4.9 (.25)	3.9 (.20)	3.6 (.19)
19.8	12.1 (.61)	6.4 (.32)	1.8 (.09)	2.3 (.11)	4.9 (.25)	3.9 (.20)	4.3 (.22)
20.1	12.1 (.60)	6.7 (.33)	2.1 (.10)	2.5 (.12)	5.4 (.27)	4.4 (.22)	4.2 (.21)
20.9	11.7 (.56)	5.4 (.26)	1.7 (.08)	2.3 (.11)	4.4 (.21)	3.7 (.18)	3.6 (.17)
21.2	12.8 (.60)	6.7 (.32)	1.8 (.08)	2.5 (.12)	5.4 (.25)	4.4 (.21)	5.0 (.24)
22.5	13.8 (.61)	7.7 (.34)	2.1 (.09)	2.4 (.11)	5.5 (.24)	4.5 (.20)	4.6 (.20)
23.2	14.0 (.60)	7.9 (.34)	2.4 (.10)	2.7 (.12)	5.6 (.24)	5.0 (.22)	5.4 (.23)
25.2	14.9 (.59)	8.8 (.35)	2.3 (.09)	2.9 (.12)	5.8 (.23)	5.0 (.20)	5.4 (.21)
25.3	15.3 (.60)	8.9 (.35)	2.5 (.10)	2.9 (.11)	6.5 (.26)	5.5 (.22)	5.6 (.22)
25.9	15.7 (.61)	8.4 (.32)	2.3 (.09)	2.8 (.11)	5.8 (.22)	5.4 (.21)	5.1 (.20)
26.3	15.6 (.59)	8.2 (.31)	2.3 (.09)	2.9 (.11)	6.1 (.23)	5.5 (.21)	6.1 (.23)
26.5	16.2 (.61)	8.2 (.31)	2.4 (.09)	2.8 (.11)	5.6 (.21)	5.3 (.20)	5.4 (.20)
27.5	16.3 (.59)	9.9 (.36)	2.4 (.09)	3.2 (.12)	6.5 (.24)	5.7 (.21)	5.7 (.21)
27.9	17.2 (.62)	8.9 (.32)	2.1 (.08)	3.0 (.11)	6.2 (.22)	5.6 (.20)	6.2 (.22)
31.5	20.4 (.65)	10.0 (.32)	2.7 (.09)	3.4 (.11)	7.7 (.24)	6.5 (.21)	7.1 (.23)
33.0	20.7 (.63)	10.7 (.32)	3.0 (.09)	3.4 (.10)	7.6 (.23)	6.7 (.20)	7.4 (.22)
37.8	24.3 (.64)	12.7 (.34)	3.2 (.08)	4.0 (.11)	10.0 (.26)	9.1 (.24)	9.3 (.25)
41.7	26.3 (.63)	14.5 (.35)	3.7 (.09)	4.1 (.10)	10.7 (.26)	9.5 (.23)	11.0 (.26)
45.0	27.5 (.61)	15.4 (.34)	3.8 (.08)	4.4 (.10)	11.4 (.25)	9.9 (.22)	11.1 (.25)

TABLE 3
Development of head spines in individual *Sebastes hopkinsi*, squarespot rockfish. "0" means spine absent, "1" means spine developing, and "-" means spine overgrown by another spine.

	Standard length (mm)																				
Spines	6.0	7.9	8.3	9.5	10.0	10.5	14.4	15.7	16.1	17.3	18.9	19.6	20.4	22.0	24.1	26.5	28.3	32.8	34.2	37.8	41.7	45.0
Nasal	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Preocular	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
Supraocular	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
Postocular	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Coronal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tympanic	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
Parietal	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Nuchal	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pterotic	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Posttemporals																						
Superior	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Inferior	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Supracleithral	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Opercular																						
Superior	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Inferior	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Preopercular																						
1st Anterior	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2nd Anterior	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3rd Anterior	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1st Posterior	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2nd Posterior	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3rd Posterior	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
4th Posterior	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
5th Posterior	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Infraorbitals																						
1st Inferior	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2nd Inferior	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3rd Inferior	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1st Superior	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-	-	-
2nd Superior	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3rd Superior	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
4th Superior	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	-	-	-	-	-	-	-

was completed at approximately 8.5 mm SL. Transformation to the juvenile stage occurred at about 20–25 mm SL. A full adult complement of dorsal, anal, and pectoral fin rays was present in fish over 9.5 mm SL. The modal counts of segmented fin rays were 15 dorsal, 7 anal, and 17 pectoral, although a dorsal ray count of 14 was almost equally common (tab. 1). Gill raker counts varied from 34 to 41, with a mode of 38. The ratios of morphometric measurements to SL were comparable in all sizes (tab. 2), indicating that body form was similar throughout the size range investigated (14.4–45 mm SL).

Head Spination

By 6.0 mm NL, the parietal, the first and third anterior preopercular, and second to fourth posterior preopercular head spines had formed on *S. hopkinsi* (tab. 3). By 7.9 mm SL, the postocular and pterotic spines were present. The fifth posterior preopercular spine was first observed at 8.3 mm SL. At 9.5 mm SL, the supracleithral, the first inferior infraorbital, and the first superior infraorbital spines were present. By 14.4 mm SL, the nasal, nuchal, post temporals, operculars, first posterior preopercular, third inferior infraorbital, and fourth superior infraorbital spines were present. At 17.3 mm SL, the preocular and third superior infraorbital were present. By 18.9 mm SL, the supraocular and tympanic spines had formed. The first superior infraorbital became overgrown by 37.8 mm SL and the fourth superior infraorbital became overgrown by 26.5 mm SL. The coronal, second anterior preopercular, second inferior infraorbital, and second superior infraorbital spines were not observed in any of our specimens.

Body Pigmentation

Prior to extrusion, *S. hopkinsi* possess pigment only along the dorsal and ventral body midlines, and ventrally and posteriorly on the gut (fig. 1A; tab. 4; Moser et al. 1977). All larvae less than 4.0 mm NL had pigment on the head and anterior of the eyes; therefore, these pigments must form soon after extrusion. It is also possible that the presence or absence of these pigments varied and the specimen shown in Moser et al. (1977) doesn't represent the full range of variation.

TABLE 4

Proportion of *Sebastes hopkinsi*, squarespot rockfish, with melanophores present at various areas averaged over 2.0 mm size bins (range of +/– 1.0 mm). SL = standard length (notochord length in preflexion specimens) in mm. Definitions of each area are given below.

SL	N	MAX	ULJ	LJ	EYE	SNOUT	OPER	CHK	NAPE	DORS	VENT	MID	HYP	DFIN	PECF	ANAL	PECB	VEB	AFB	PEDB
3	18	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5	19	0.0	0.1	0.1	0.0	1.0	0.0	0.0	0.0	1.0	1.0	0.2	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
7	11	0.0	0.0	0.3	0.0	1.0	0.0	0.0	0.0	1.0	1.0	0.4	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0
9	2	0.5	0.0	1.0	0.0	1.0	1.0	0.0	0.5	1.0	1.0	0.5	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0
11	2	1.0	0.0	1.0	0.0	1.0	1.0	0.0	0.0	1.0	1.0	1.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
13	2	0.5	0.0	1.0	0.0	1.0	1.0	0.0	0.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
15	5	0.8	0.2	1.0	0.2	1.0	1.0	0.0	0.2	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
17	11	0.9	0.1	1.0	0.6	1.0	1.0	0.0	0.6	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
19	14	1.0	0.9	1.0	0.9	1.0	1.0	0.0	0.9	1.0	1.0	1.0	1.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
21	9	1.0	0.6	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
23	14	1.0	0.9	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.1	0.1	0.0	0.1	0.0	0.0	0.0
25	12	1.0	0.9	1.0	1.0	1.0	1.0	0.1	1.0	1.0	1.0	1.0	1.0	0.5	0.0	0.0	0.4	0.0	0.0	0.2
27	9	1.0	1.0	1.0	1.0	1.0	1.0	0.2	1.0	1.0	1.0	1.0	1.0	0.9	0.0	0.0	1.0	0.2	0.3	0.8
29	11	1.0	0.8	1.0	1.0	1.0	1.0	0.2	1.0	1.0	1.0	1.0	1.0	0.8	0.1	0.0	0.6	0.3	0.3	0.5
31	10	1.0	1.0	1.0	1.0	1.0	1.0	0.1	1.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.8	0.3	0.5	0.7
33	4	1.0	1.0	1.0	1.0	1.0	1.0	0.8	1.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.8	0.5	1.0	1.0
35	2	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.5	0.0	1.0	0.5	0.5	0.5
37	4	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.8	0.5	1.0	1.0	1.0	1.0
39	9	1.0	1.0	1.0	1.0	1.0	1.0	0.9	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.8	1.0	1.0	1.0	1.0
41	8	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.8	1.0	1.0	1.0	1.0
43	16	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
45	10	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
47	10	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
49	15	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
51	9	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

MAX=side of maxilla, ULJ=under lower jaw, LJ=anterior tip of lower jaw, EYE=posterior-ventral edge of eye orbit, SNOUT=dorsal surface anterior to eye, OPER=operculum, CHK=radiating cheek bars, NAPE=nape, DORS=dorsal body, VENT=ventral body, MID=along lateral midline, HYP=hypural region, DFIN=spinous dorsal fin, PECF=pectoral fin blade, ANAL=anal fin blade, PECB=body bar at pectoral fin, VEB=body bar at vent, AFB=body bar at anal fin, PEDB=body bar at peduncle.

Pigment on the tip of the lower jaw and along the lateral midline was first observed in fish approximately 5.0 mm NL with all fish having lower jaw pigment by 9.0 mm SL and lateral midline pigment by 11 mm SL (tab. 4). Pigment formed on the maxilla and operculum by 9.0 mm SL. Pigment along the bases of the dorsal-most pectoral fin rays was observed in six fish from 6–10 mm SL, but otherwise was absent before the juvenile stage. Among larvae less than 10 mm SL, only one specimen each had pigment under the lower jaw and along the nape.

By 10.5 mm SL, pigment on the head and anterior to the orbit had intensified and merged to form a continuous pigment patch (fig. 1B; tab. 4). Pigment along the tip of the lower jaw became denser and began to extend posteriorly. Maxillary pigment also was denser compared to smaller specimens. Dorsal and ventral midline melanophores increased in number and intensity and extended anteriorly. Dorsal midline pigment occurred from the caudal peduncle to the second anterior dorsal spine, while ventral midline pigment was present from the caudal fin to the base of the posterior-most anal fin rays. A few melanophores were present along the lateral midline on the caudal peduncle in all specimens. Hypural pigment had begun to form with a few melanophores along the edge of the lower hypural plate. Pigment was not observed on any of the fins, but pigment on the axillary surface of the pectoral fin base was present in all specimens.

At 14.4 mm SL, pigment along the tip of the lower jaw, maxilla, and anterior orbital area intensified and increased in density (fig. 1C; tab. 4). Head pigment intensified and covered the entire dorsal surface. Opercular pigments increased in number, sparsely covering the dorsal surface of the operculum. Dorsal midline pigment increased in density and spread forward to the first or second anterior dorsal spine. However, ventral midline pigment changed little in fish ranging from 12–16 mm SL, and even decreased in some individuals. A few melanophores were added anteriorly at the bases of some of the anal fin rays. Hypural pigment strengthened and was present in all specimens ≥13 mm SL. Lateral midline pigment intensified and progressed both anteriorly and posteriorly compared to smaller specimens, extending from the hypural edge to below the dorsal soft rays.

At 19.4 mm SL, pigment along both jaws increased in number and progressed posteriorly (fig. 1D; tab. 4). Pigment on the ventral surface of the lower jaw increased in number and covered a wider area. Pigment had formed along the nape and merged with the head, snout, upper jaw, and dorsal midline pigments to form a continuous

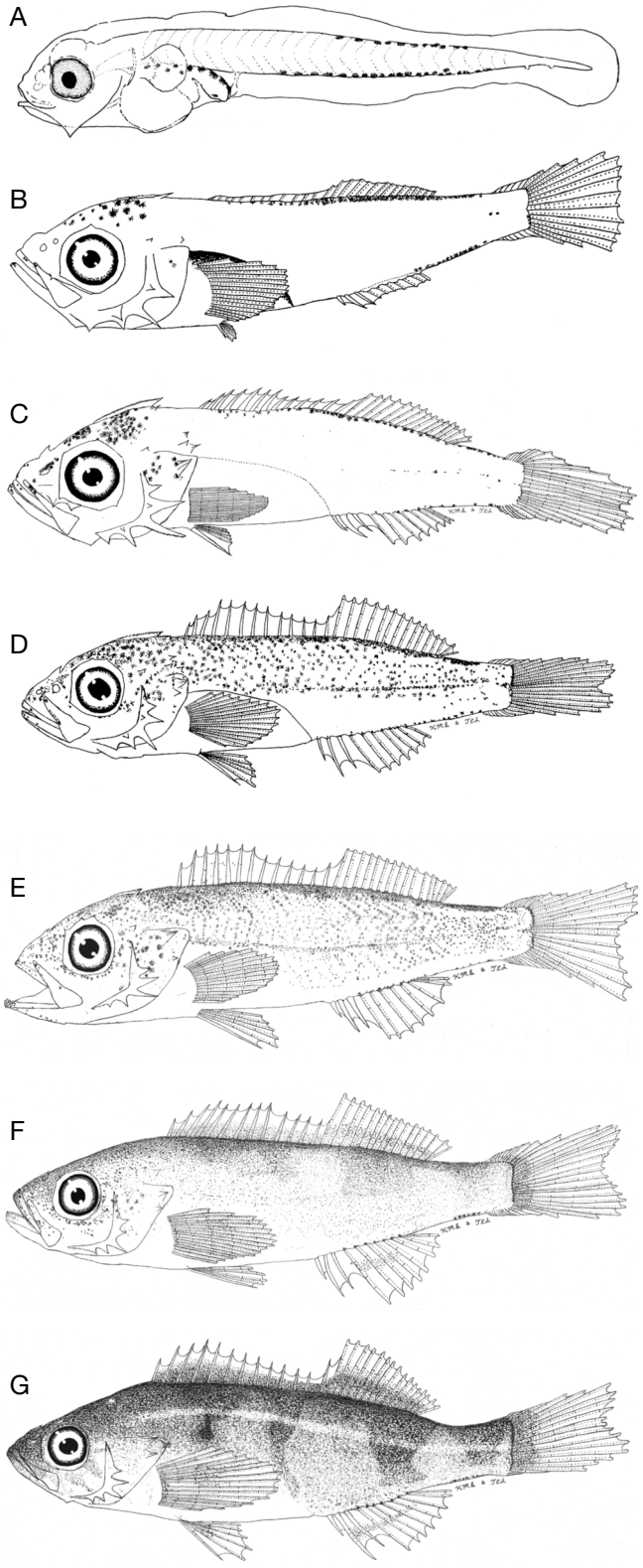

Figure 1. Developmental series of *Sebastes hopkinsi*, squarespot rockfish. (A) 4.7 mm SL preextrusion larva (from Moser et al. 1977); (B) 10.5 mm SL larva; (C)14.4 mm SL larva; (D) 19.4 mm SL pelagic juvenile; (E) 26.9 mm SL pelagic juvenile; (F) 36.9 mm SL pelagic juvenile; (G) 45.0 mm SL pelagic juvenile. Illustrations B-G drawn by authors. Note that not all head spines are included in the illustrations.

band from the tip of the jaw to the caudal fin. Head, nape, and opercular pigment intensified and merged to cover the upper half of the head (fig. 1D). Melanophores appeared along the posterioventral edge of the orbit. The dorsal half of the body was dotted with pigment, although no body bars had yet appeared. The lateral midline pigment stretched from the caudal fin to the gut, almost forming a continuous line. Hypural pigment continued to intensify, especially on the dorsal region. Ventral midline pigment stretched from the caudal fin to the first anal spine and increased in density. All fins remained unpigmented in specimens from 17–21 mm SL, except for one specimen (19.1 mm SL) that had a few melanophores in the spinous dorsal fin. The ventral half of the body remained only lightly pigmented.

By 27 mm SL, the dorsal half of the body was heavily pigmented, except for an unpigmented area below the dorsal midline of the caudal peduncle (fig. 1E; tab. 4). More of the ventral half of the body was pigmented than in smaller specimens. The spinous dorsal fin was pigmented in 90% of the specimens, with melanophores on the membranes between the anterior-most spines. All other fins remain unpigmented. Cheek bars had begun to form on a few specimens by 27 mm SL. Hypural pigment became a thick band along the distal margin. The ventral midline was much less pigmented than the dorsal midline. The dorsal half of the anterior-most body bar (at the pectoral fin) was evident in most fish. The other body bars began to form in a few specimens.

At 37 mm SL, juveniles had pigment covering most of the body (fig. 1F; tab. 4). The hypural, dorsal midline, nape, head, snout, and maxilla pigments were all well developed and formed a broad, dark band from the caudal fin to the mouth. The lower jaw and maxilla pigments formed a ring around the mouth. Circumorbital pigment had increased compared to smaller fish. Both cheek bars were present, but incomplete. The lower halves of both the spinous and soft dorsal fins were pigmented throughout the entire length of the fin. Pectoral fin pigment was present in 80% of the specimens between 35 and 39 mm SL, occurring from the base of the fin out about halfway to the distal edge. The anterior portion of the caudal fin was pigmented. The anal fin was pigmented in half of the specimens, with a pigment stripe occurring from about the midpoint of the fin (fig. 1F). The pelvic fins remained unpigmented. Body bars were forming at the caudal peduncle, under the soft dorsal fin, above the vent, and above the pectoral fin. The caudal and anal fin body bars were prominent in all specimens.

At 45.0 mm SL, *S. hopkinsi* juveniles remained heavily pigmented along the dorsal half of the body with the ventral region much less pigmented (fig. 1G; tab. 4). The dorsal midline, nape, head, snout, maxilla, lower jaw, ventral surface of the lower jaw, and hypural pigments were

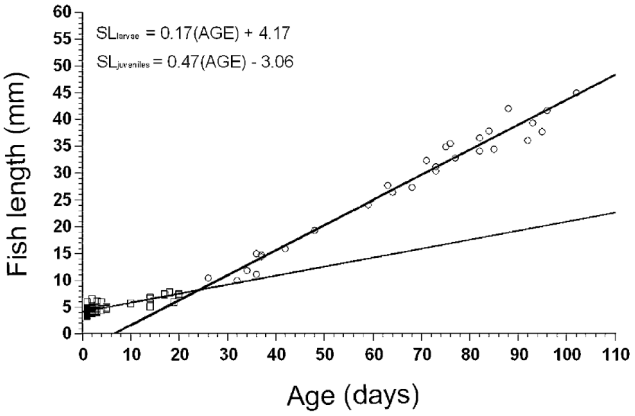

Figure 2. Relationship between fish standard length (notochord length below 9.0 mm) and age for *Sebastes hopkinsi*, squarespot rockfish (n = 116). Open squares represent larvae (n = 85), open circles represent juveniles (n = 31), and solid lines represent predicted values from each relationship.

all dense and surrounded much of the fish in a thick, dark band. The ventral midline pigment was much less dense than in smaller specimens and only reached from the caudal fin to the third anal spine. The area from the vent to the eye, including the gut area, was only lightly pigmented, with the heavier pigmentation on the operculum and in the two cheek bars, which were clearly visible by this size. All four body bars were well developed, with each stretching ventrad from the dorsal midline, but stopping short of the ventral midline. All of the fins were pigmented. The dorsal, caudal, and pelvic fins were pigmented proximally, leaving the tips clear of pigment. Pigment in the anal fin consisted of a horizontal stripe about midway through the fin, stretching from the first spine to the sixth ray. The pectoral fin was pigmented proximally and in an area in the middle of the fin.

Otolith Examination

A total of 116 otoliths were examined from larval and juvenile *S. hopkinsi* ranging in length from 3.5–45.0 mm SL and in age from 1 to 92 days. Two linear relationships were found to exist between SL and age (as estimated from otolith increment counts); one for preflexion and flexion larvae (slope = 0.17 mm/d; intercept = 4.17 mm; r^2 = 0.66; n = 85; fig. 2) and one for postflexion larvae and juveniles (slope = 0.47 mm/d; intercept = –3.06 mm; r^2 = 0.97; n = 31; fig. 2). The two linear relationships were considered the best model because of the differential growth between postflexion and preflexion larvae (Laidig et al. 1991; Sakuma and Laidig 1995; Laidig et al. 1996). The radius of the extrusion check ranged from 12.4 to 13.8 µm, averaging 13.2 µm (SD = 0.34; n = 23). Accessory primordia first appeared in the otolith of a 24.2 mm specimen and were present in all larger specimens. The average increment count at the beginning of the innermost accessory primordium was 53 (n = 20). This equates to a size of 21.8 mm SL using the above length-and-age relationship for fish that completed flexion. Based on these characters, transition from the larval to juvenile phase begins at approximately 22 mm SL.

Molecular Identification

Phylogenetic analysis of the cytochrome-*b* gene, comparing unknowns to sequences from all eastern Pacific *Sebastes* spp., grouped all juveniles identified by morphology as *S. hopkinsi* with reference samples of *S. hopkinsi* and *S. ovalis* (speckled rockfish; minimum evolution tree, Kimura 2 parameter model as implemented in MEGA v2.1 [Kumar et al. 2001], 1000 bootstrap replicates, 99% bootstrap support). Additionally, all samples shared a genetic polymorphism at position 246 of the cytochrome-*b* gene, which is unique to *S. hopkinsi* and *S. ovalis*. These two species are closely related and can only be reliably separated genetically by an autapomorphic nucleotide substitution for *S. ovalis* at position 543 of the cytochrome-*b* gene (J. Hyde unpublished data). There was a high degree of intra-specific variation at this gene (4.2%, n = 37) for *S. hopkinsi* while this variation was much reduced (0.26%, n = 15) for *S. ovalis* (J. Hyde unpublished data). Due to the high degree of intra-specific variation for *S. hopkinsi*, unless a sequence matched 100% with that of the reference sequences, the diagnostic nucleotide at base 543 was used to distinguish between *S. hopkinsi* (A) and *S. ovalis* (T). Three of the fish examined in this study (MI11, MI12, and MI17) matched 100% with the sequence from reference specimens, while the remainder differed from the closest reference specimen by one to seven nucleotides (0.13–0.90% sequence divergence; fig. 3).

DISCUSSION

Sebastes hopkinsi have distinctive pigment patterns at different sizes. Large juvenile *S. hopkinsi* had a four-bar pattern, while smaller juveniles had diffuse pigment over most of their bodies. Larvae tended to be pigmented mainly on the head and along the dorsal midline, with some lateral midline and pectoral fin pigment present in some individuals. Modal counts of segmented fin rays were seven for the anal fin, 17 for the pectoral fin, and 14 or 15 for the dorsal fin. By using a combination of pigment characters and fin ray counts, more accurate field and laboratory species identifications can be achieved.

By using fin ray and gill raker counts, only 10 *Sebastes* spp. could be confused with *S. hopkinsi* at sizes greater than 15 mm SL. Five of these (*S. flavidus*, *S. goodei*, *S. proriger* [redstripe rockfish], *S. wilsoni* [pygmy rockfish], and *S. zacentrus* [sharpchin rockfish]) can be separated from *S. hopkinsi* after about 18 mm SL by their lack of a supraocular spine. Five species (*S. semicinctus* [halfbanded

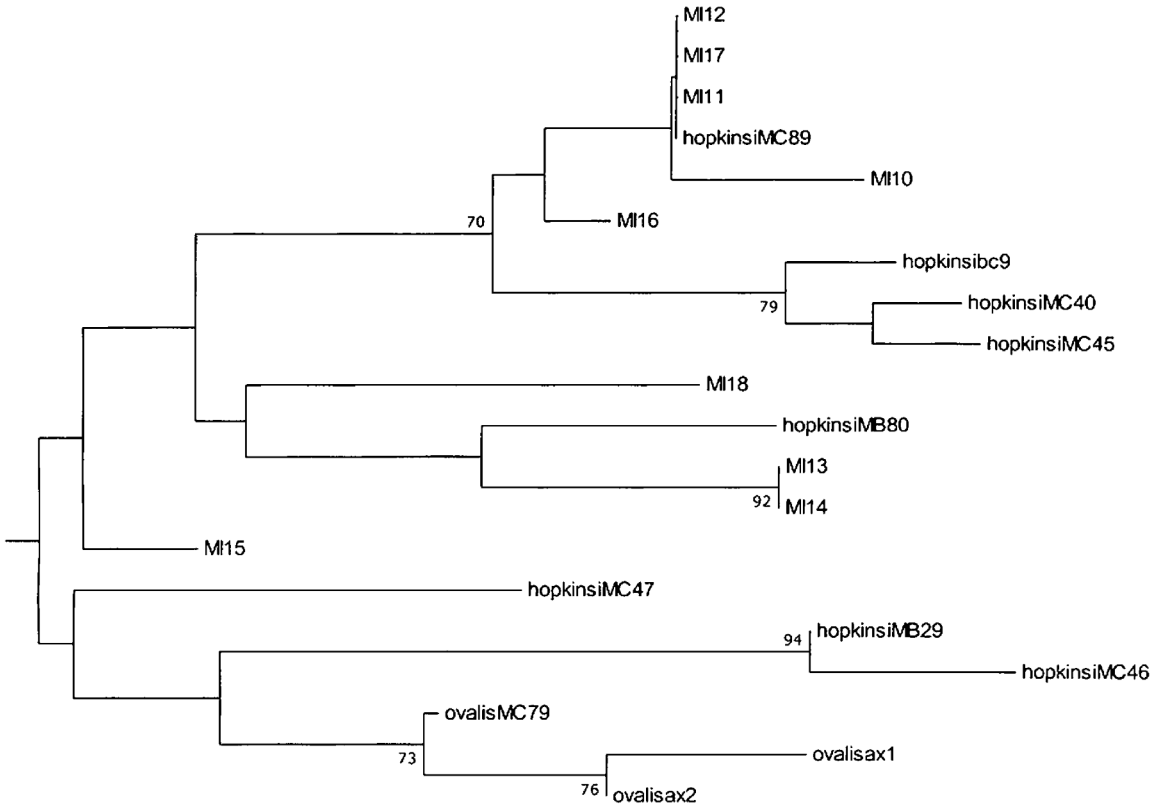

Figure 3. Sub-tree of a Minimum Evolution tree generated from the first 782bp of the mitochondrial cytochrome-*b* gene with the Kimura 2-parameter distance model MEGA v2.1, 1000 bootstrap replicates. Juvenile *Sebastes hopkinsi*, squarespot rockfish, described in this study are denoted as MI10-MI18. Haplotypes from reference specimens are denoted with the species name followed by unique 3- or 4-character identifiers (e.g., ovalisAX2 is *S. ovalis* sample # AX2). Branch nodes with greater than 70% bootstrap support values are labeled.

rockfish], *S. pinniger*, *S. miniatus* [vermilion rockfish], *S. entomelas*, and *S. alutus* [Pacific Ocean perch]) cannot be separated from *S. hopkinsi* by fin ray counts, gill raker counts, or by the presence of a supraocular spine. *Sebastes semicinctus* has only about a 15% overlap in dorsal fin ray counts, with a mode of 13 compared to counts of 14 and 15 for *S. hopkinsi* (Laroche[1]). Using this in combination with the distinctive barring patterns of both *S. semicinctus* and *S. hopkinsi*, the two species can be separated. *Sebastes pinniger* and *S. miniatus* can be distinguished by their distinctive pigmentation patterns and their distinctive body shapes (Matarese et al. 1989). Postflexion larvae of both species are distinctly deeper-bodied than *S. hopkinsi* and, up to 15 mm SL, both species have little dorsal body pigment, except where it has coalesced into dark patches near the dorsal midline (*S. pinniger*) or anteriorly into a broad saddle (*S. miniatus*). This contrasts with the thick band of dorsal body pigment that is present in late larval *S. hopkinsi*. By 25 mm SL, two saddles cover most of the body in *S. miniatus*, easily distinguishing it from *S. hopkinsi*. *Sebastes pinniger* remains lightly pigmented until the late juvenile stage after settlement to the benthos, and would therefore not be confused with *S. hopkinsi*. *Sebastes entomelas* has pigmented pectoral and pelvic fins, with more extensive pectoral pigmentation then those individuals of *S. hopkinsi* having pectoral pigment. Pelagic juveniles also have a distinctive saddling pattern on the dorsal half of the body, and a black spot in the spinous dorsal fin (Laroche and Richardson 1981). This pattern is easily discernable from the *S. hopkinsi* pigment pattern. The modal pectoral fin ray counts differ between *S. alutus* (18 fin rays) and *S. hopkinsi* (17 fin rays), with only a 4% overlap. There is only a 7% overlap in anal fin ray counts. Only two published illustrations exist for *S. alutus*; one at the preflexion stage and one for a 57 mm SL juvenile *S. alutus* (Laroche[1]), making it difficult to compare pigmentation with *S. hopkinsi*. However, because *S. alutus* has uniform mottling covering the body as a late-stage juvenile, and *S. hopkinsi* has a barred pattern in fish greater than 30 mm SL, the presence of bars should allow separation. Capture location may also aid in this differentiation, with *S. alutus* ranging from Baja California north (uncommon south of northern California) and *S. hopkinsi* ranging from southern Oregon south, but rare north of Monterey (Love et al. 2002). Caution must be used with species ranges because larvae and juveniles are pelagic and may have a broader geographic range than the adults.

Using fin ray and gill raker counts, supraocular spine presence, and general pigment patterns, *S. hopkinsi* can be separated from other species at sizes greater than 15 mm SL with a relatively high degree of certainty.

Compared to the few species similar to *S. hopkinsi* at larger sizes, many species can be confused with *S. hopkinsi* at sizes less than 15 mm SL. Fin ray counts can be useful at sizes greater than 8 mm SL, while head spine and gill raker counts are unreliable for most larvae. Based on fin ray counts alone, 27 species could be confused with *S. hopkinsi* at small sizes. Some of these species have distinctive pigmentation and can be separated from *S. hopkinsi*, leaving 11 species to consider. Two of these species primarily occur farther north, and five spawn later in the year (Love et al. 2002); only *S. maliger* (quillback rockfish), *S. nebulosus* (china rockfish), *S. ovalis*, *S. ruberrimus* (yelloweye rockfish), and *S. semicinctus* cannot reliably be separated from *S. hopkinsi* at 8–15 mm SL. Larval illustrations of these five species are not sufficient to distinguish them from *S. hopkinsi*, and each of these species has at least one overlapping fin ray count with *S. hopkinsi*.

At sizes less than 8 mm SL, pigmentation, timing of parturition, and location of capture can be used to differentiate between some, but not most, species. Many species are poorly illustrated at small sizes, and the distinctions between species are slight to nonexistent for many individuals. Small *S. hopkinsi* cannot be reliably separated from *Sebastes* spp. of the subgenus *Pteropodus* except by the use of DNA (Taylor and Watson 2004; Watson and Robertson 2004). Identifications of distinct species based on pigmentation may never be obtained at these small sizes.

The identification of larval and juvenile *S. hopkinsi* was confirmed using DNA sequence analyses. Only one species, *S. ovalis*, was grouped with *S. hopkinsi*. Among *Sebastes*, these species uniquely share a genetic polymorphism at position 246 of the cytochrome-*b* gene, and belong to the same subgenus, *Acutomentum*. They can be reliably separated by an autapomorphic nucleotide substitution for *S. ovalis* at position 543 of the cytochrome-*b* gene. At birth, *S. ovalis* closely resemble *S. hopkinsi*, but they may develop heavier pectoral fin pigmentation during the preflexion stage (Moser et al. 1977); however, the pigment pattern for most of the early life history of *S. ovalis* is presently unknown.

The high genetic diversity in *S. hopkinsi* and the geographic differences in collection sites for the larval and juvenile *S. hopkinsi* may confound identification of the species (and subsequent separations from other *Sebastes* spp.). These factors may also lead to changes in pigmentation in larval stages. Sakuma et al. (2005) reported variability in pigmentation in *S. jordani*, a species with low genetic diversity. However, the differences in pigmentation did not preclude the authors from distinguishing *S. jordani* from other species. Data from the current study cannot adequately address pigmentation differences in *S. hopkinsi*, and further study will be needed to determine if genetic or geographic differences will have an influence on the identification of *S. hopkinsi*.

The radius of the extrusion check can be a useful character for differentiating *Sebastes* spp. (Laidig and Ralston 1995). In this study, the radius of the extrusion check ranged from 12.4–13.8 μm, averaging 13.2 μm (SD = 0.34). Of the other sixteen *Sebastes* spp. with measurement information for the extrusion check radius (Laidig and Ralston 1995; Laidig et al. 1996; Laidig and Sakuma 1998; Laidig et al. 2004), three had radii much larger than *S. hopkinsi*, and eight had radii much smaller than *S. hopkinsi*. That leaves five species with similar radii: *S. auriculatus* (14.1 μm, SD = 1.5), *S. flavidus* (12.1 μm, SD = 0.7), *S. entomelas* (11.8 μm, SD = 0.9), *S. paucispinis* (12.2 μm, SD = 1.1), and *S. rastrelliger*, grass rockfish (14.0 μm, SD = 0.4). Among these, all but *S. entomelas* can be distinguished from *S. hopkinsi* using meristics and head spination, and all five species can be differentiated from *S. hopkinsi* using pigmentation at sizes greater than 8 mm SL. At smaller sizes, the extrusion check radius may be helpful in eliminating *S. hopkinsi* as a possibility in groups of unknown larvae, but it cannot be used to specifically identify a larva as *S. hopkinsi*, because the size of the extrusion check radius is not known for all *Sebastes* spp.

The daily growth rate of juvenile *S. hopkinsi* was 0.47 mm/day, which is similar to the growth rates of other juvenile *Sebastes* spp. The fastest growth rates were recorded for juvenile *S. paucispinis*, (0.56–0.97 mm/day) and *S. jordani* at (0.52–0.64 mm/day) (Laidig et al. 1991; Woodbury and Ralston 1991). Growth rates of *S. goodei* (0.40–0.56 mm/day) and *S. entomelas* (0.30–0.60 mm/day) are similar to *S. hopkinsi* (Woodbury and Ralston 1991). *Sebastes rastrelliger* (0.36 mm/day; Laidig and Sakuma 1998), *S. saxicola* (stripetail rockfish; 0.37 mm/day; Laidig et al. 1996), and *S. wilsoni* (0.28 mm/day; Laidig et al. 2004) all have slower growth rates. The slower rate (0.17 mm/day) in this study for larval *S. hopkinsi* that had not completed notochord flexion is similar to that in previous studies of *Sebastes* growth during their first month of life (Laidig et al. 1991; Sakuma and Laidig 1995; Laidig et al. 1996).

The ability to correctly identify rockfish larvae and juveniles is important for developing accurate species recruitment indices. Recruitment data can be used to determine population biomasses through larval production models (Ralston et al. 2003), and have proven useful in stock assessments (MacCall et al. 2002). Currently, there are pigment descriptions of larval and juvenile stages for only approximately 50% of the *Sebastes* spp. occurring

along the west coast of North America. Further work is needed to describe the remaining unidentified life history stages of over 30 species.

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CATCH STRATEGIES FOR THE PACIFIC SARDINE (*SARDINOPS SAGAX*)

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ABSTRACT

In this paper we develop a model of the long-term prospects for the Pacific sardine (*Sardinops sagax*) in which the surplus growth of the stock is influenced by random fluctuations. This can have an enduring effect partly through a serial correlation in the environmental disturbances, but also, and more importantly, because the effect of these random disturbances is related to the size of the stock itself. We use the model to generate fluctuations in the sardine stock to compare alternative fishing strategies: (i) constant escapement; (ii) constant exploitation rate; and (iii) a hybrid of the two. We find that strategy (i) results in greater catches per year and greater variability than (ii). The hybrid, (iii), results in greater catches and greater variability than (i). We conclude that the model supports the existing management of the U. S. Pacific sardine fishery.

INTRODUCTION

In the 1930s and 1940s the Pacific sardine (*Sardinops sagax*) supported one of the largest fisheries not just in the United States but the whole world (fig. 1). In the 1940s and 1950s the landings declined steeply despite a short recovery around 1950, and in the early 1960s the fishery stopped. Parallel to the decline in landings the stock also declined, which initially was blamed on overfishing. Later research has, however, indicated that in the past, and long before any fishing began, the sardine stock has been subject to similar crashes (Baumgartner et al. 1992). Overfishing thus may not have been the sole cause of the decline of the sardine stock in the 1930s and 1940s, and it might have declined in any case due to natural reasons.

This suggests that a model of the long-term prospects of the Pacific sardine must be capable of generating a collapse of the sardine stock in the absence of any fishing. Such a model must rely on either explicit environmental variables that can generate such fluctuations or other mechanisms, possibly related to the sardine stock itself. This paper examines a model of this kind in which the surplus growth of the stock is influenced by a random variable that generates fluctuations in stock size. These fluctuations can have an enduring effect partly through a serial correlation in the environmental disturbances but also, and more importantly, because the effect of these fluctuations is related to the size of the stock itself. The random disturbances will be calibrated based on the history of the stock.

The main purpose of the model is to generate fluctuations that resemble those that may be expected to occur in reality, in order to compare the effect of alternative fishing strategies. The model does not attempt to explain the fluctuations in the sardine stock, as it does not incorporate any physical processes that would generate such fluctuations. From the history of the sardine fishery and the sardine stock it is clear that fluctuations in the environment strongly influence stock development whatever the underlying physical factor is. To the extent the model generates realistic fluctuations in the stock, it suggests that just a few unlucky draws of nature are all that's needed to produce long periods of low stock abundance, such as have occurred in the past. It takes a long time for the stock to recover from such declines, simply because a small stock generates little growth. Hence, long waves of climate fluctuations, referred to as regime shifts, may not be necessary to produce prolonged periods of low stock abundance. As an illustration, suppose the stock has been knocked down to 5,000 metric tons (mt), which is believed to be its low point during the 1960s and 1970s. With a growth rate of 40% per year it would take the stock 16 years to recover above 1 million mt. In its heyday in the 1930s and 1940s it was well above that level. Such a high growth rate was observed in the 1980s and 1990s, a period of favorable environmental conditions (PFMC 1998, Appendix B).

How, then, should a stock subject to such dramatic random fluctuations be managed? We shall compare two alternative fishing strategies, one that attempts to always leave behind a certain minimum stock for growth and reproduction (target escapement), and one that catches a certain share of the stock available each year (constant fishing mortality). In addition we will look at a hybrid of these, one in which a certain share of the stock beyond a certain minimum is caught each year. This is to approximate the strategy currently employed in the management of the Pacific sardine under the U. S. Pacific

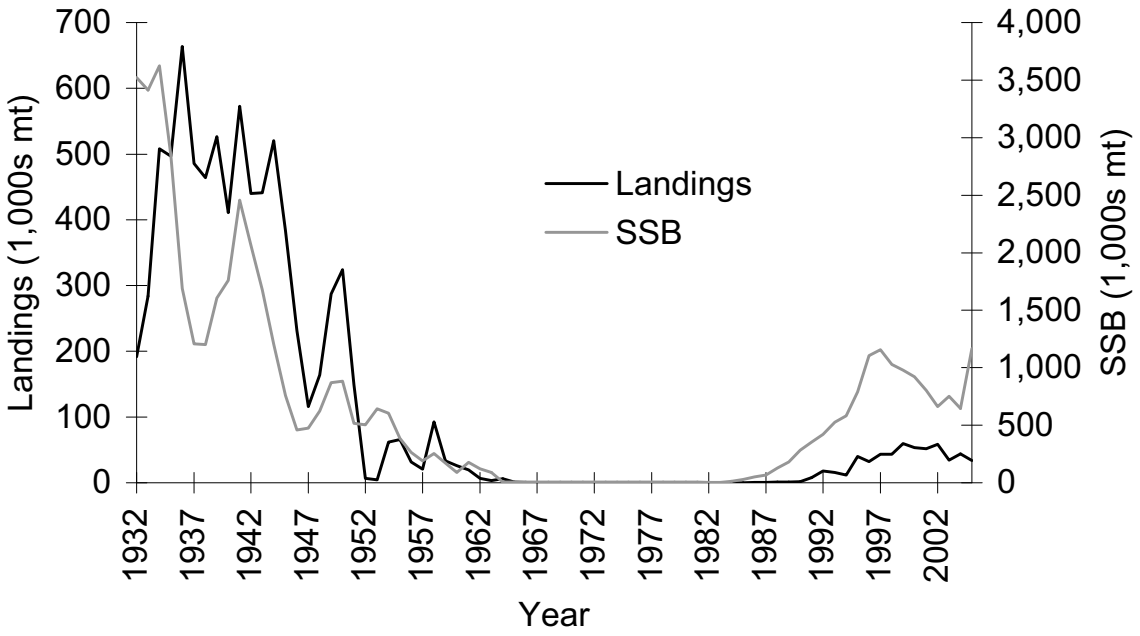

Figure 1: Spawning stock biomass (SSB) and landings (in California) of Pacific sardines (*Sardinops sagax*).

Fishery Management Council's (PFMC) Coastal Pelagic Species Fishery Management Plan (PFMC 1998, Appendix B), where the share of the stock that the industry is allowed to catch every year depends on environmental conditions, measured as the average sea surface temperature for the three most recent years. To mimic that strategy, we let the share being taken depend on the realized random environmental variable for the two most recent years.

The alternative strategies will be compared based on the average fish catches they would generate over a long time period and on the variability in the catches, measured as standard deviation and maximum and minimum annual catches. The variability of catches is also reflected in the number of years without fishing, either because there is virtually no fish to be caught or because the stock is below the escapement target.

Using stochastic models to analyze alternative fishing strategies for the sardine stock is not novel. In the management plan for sardine (PFMC 1998, Appendix B), a stochastic model, different from the one used here, was employed to simulate the development of the stock under different exploitation rates: target escapement and maximum catches. Since there is considerable uncertainty about what kind of model would be most appropriate for the sardine stock, it is of interest whether both models produce similar results with respect to the relevant management criteria.

The present model is a simple one, being a surplus growth model without any age structure. Nevertheless, such models can be useful to study the implications of alternative management strategies and related issues. An approach similar to the one taken here could be useful not only for other pelagic stocks that are highly variable; for example, it has been applied to study the implications of overfishing of the northeast Arctic cod (Hannesson 2007).

THE MODEL

Data on catches and the (spawning) stock of the Pacific sardine go back to 1932[1]. From these it is possible to calculate the surplus growth in year t as the difference in stock size between year $t+1$ and t plus the catches of fish in year t. According to Jacobson et al. (2005) only 83% of landings in any year represent surplus growth (some fish that were caught would have died for natural reasons). We shall follow that procedure here.

Figure 2 shows the surplus growth and the spawning stock of the Pacific sardine 1932–2004. Clearly the surplus growth is largely independent of the stock size, but it also appears that the variability in surplus growth increases with the stock, up to a point. A logistic surplus growth function was estimated by minimizing the sum of squared differences between the curve and the cal-

[1]California sardine landings for the period 1932–80 are from the PFMC's Coastal Pelagic Species Fishery Management Plan (PFMC 1998, Appendix A); sardine landings for 1981–2005 are from the PacFIN management database. Pacific sardine spawning stock biomass estimates for the period 1932–2000 are from Amendment 10 to the PFMC's Coastal Pelagic Species Fishery Management Plan (PFMC 2002, Appendix C); sardine biomass estimates for 2001–05 are from the PFMC's annual stock assessment and fishery evaluation document for coastal pelagic species (PFMC 2007).

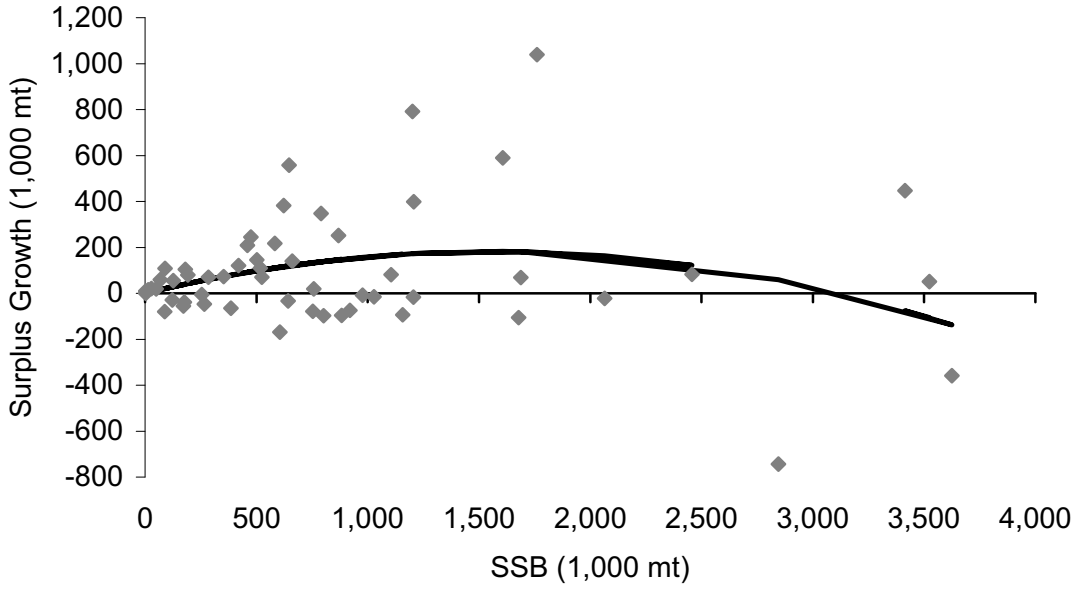

Figure 2: Surplus growth and spawning stock of Pacific sardine (*Sardinops sagax*) 1932–2004, and the estimated surplus growth curve.

culated surplus growth. This curve is also shown in Figure 2 and has the parameters $r = 0.2337$ and $K = 3121$.[2]

The next step is to define fluctuations in surplus growth as deviations (D) from the surplus growth curve, giving:

$$D_t = G_t - rS_t\,(1 - S_t/K), \tag{1}$$

where G is the calculated surplus growth, shown by the points in Figure 2, and S is the stock. Behind this deviation is the realization of a random environmental variable. However, the environmental variable is not what we observe but how it translates into surplus growth. Figure 2 suggests, as the curve indicates, that good or bad environmental conditions have a larger impact on surplus growth as the stock increases up to a certain point, but a diminishing impact after that. To elicit the environmental variable, we estimate the absolute value of D as, respectively, a quadratic versus a logarithmic function of S:

$$|D| = aS - bS^2; \tag{2}$$

$$ln|D| = \alpha + \beta lnS\,. \tag{3}$$

Table 1 shows the results of estimating these parameters by ordinary least squares. All parameters except α are highly significant, indicating that the deviations in surplus growth increase with the stock but either decline beyond a certain stock level (Equation 2) or increase with the stock at a diminishing rate (Equation 3). In the following we will use both equations and refer to them as the quadratic (Equation 2) versus logarithmic (Equation 3) model.

TABLE 1
Estimated parameters of how variations in surplus growth depend on stock size.

Parameter	Estimate	*t*-value
a	0.295	7.3
b	5.6733E-05	3.8
α	0.1633	0.2
β	0.6914	5.5

By dividing D by the right-hand side of Equation 2 versus Equation 3, we can calculate the environmental disturbance (U) which caused the deviation in the surplus growth:

$$U_t = \frac{D_t}{aS_t - bS_t^2}\;; \tag{4}$$

$$U_t = \frac{D_t}{S_t^{\beta} e^{\alpha}}\;. \tag{5}$$

The pattern in the data indicates that the disturbances are serially correlated. Regression analysis supports this for both models, although for the quadratic model, the support is weak (critical p-value 0.054). Using the estimates in Table 2, we can calculate the pure random disturbance each year (V_t):

$$V_t = U_t - k - mU_{t-1}\;, \tag{6}$$

[2]A linear regression of surplus growth on the spawning stock and spawning stock squared gives virtually identical results, and both parameters (r and r/K) are statistically significant.

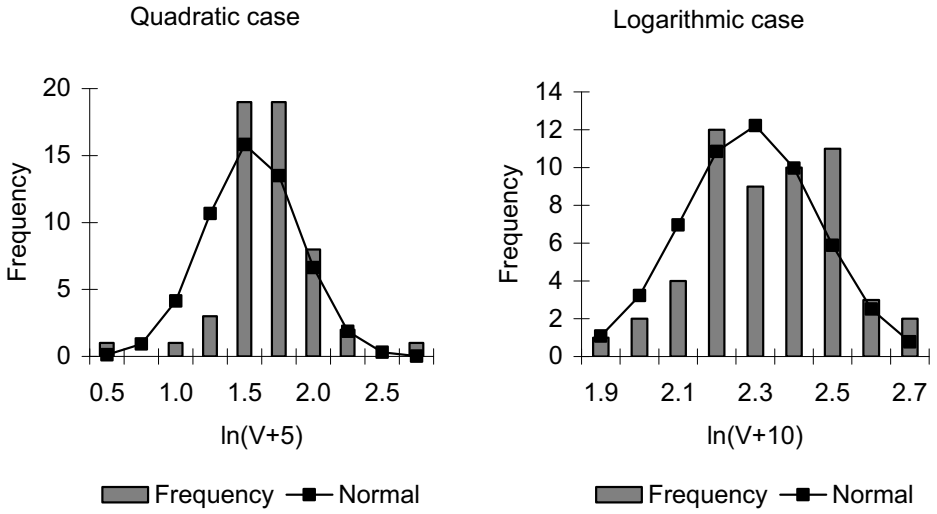

Figure 3: Histogram of *lnV* transformed and a normally distributed variable with the same mean and variance.

TABLE 2
Estimates of serial correlation in environmental disturbances ($U_t = k + mU_{t-1}$), *p*-values in parentheses.

Model	*k*	*m*
Quadratic (Eq. 2)	0.1709 (0.507)	0.2677 (0.054)
Logarithmic (Eq. 3)	0.0658 (0.791)	0.3334 (0.019)

with U_t being determined from Equation 4 or Equation 5, depending on whether we are using the quadratic or the logarithmic model (Equation 1 or 2). After a suitable linear transformation, the logarithms of the *V*s are close to normally distributed, as shown in Figure 3.

Using normally distributed random numbers to generate *lnV* and the serial correlation to generate *U*, we are able to generate quite varied development patterns for the sardine stock in the absence of fishing[3]. Three different runs for each of the above models are shown in Figures 4 and 5. What is worthy of note is the possibility of generating crashes of the stock, after which it persists at a very low level until recovery slowly succeeds. Such patterns seem to have occurred in the past (Smith 1978; Baumgartner et al. 1992) and certainly describe the development of the stock after the moratorium in the 1960s and until recovery set in around 1990. Some runs produce cycles, and in some the stock varies around a level close to the average carrying capacity ($K = 3121$) without much of a trend. If anything, the quadratic model seems better able to produce crashes that persist for decades, like the one from the 1960s to about 1990[4]. One difference between the two models is that the stock

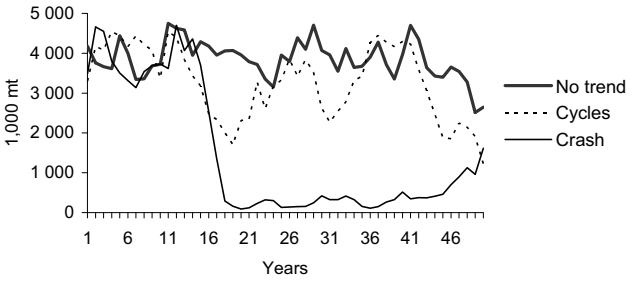

Figure 4: Alternative patterns for the stock produced by three runs of the quadratic model without fishing over a 50 year period.

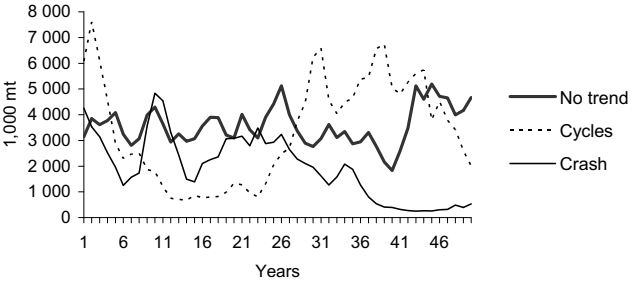

Figure 5: Alternative patterns for the stock produced by three runs of the logarithmic model without fishing over a 50 year period.

can become considerably greater in the logarithmic model than in the quadratic model. The reason is that a random draw of an advantageous environmental variable always increases surplus growth in the logarithmic model, but less and less the larger the stock is. In the quadratic

[3]There is in principle no upper or lower bound to the normally distributed random variable. We have precluded extinction of the stock due to an extremely unfavorable environment by imposing the restriction that the stock can never fall below 5,000 mt, the assumed minimum in the 1960s and 70s. Extremely favorable environmental conditions can occur, but with a low probability.

[4]A referee pointed out that the occasionally very high stock levels produced by the logarithmic model agree with the evidence from scale sediments that the sardine stock has in earlier times reached higher peaks than in the 1930s (Smith 1978; Baumgartner et al. 1992), and that the occasional peaks of the Japanese and the Humboldt sardine stocks lend credence to the logarithmic model.

model, a large stock is directly counterproductive, leading to a smaller surplus growth for any draw of the environmental variable.

TARGET ESCAPEMENT VERSUS CONSTANT FISHING MORTALITY

What are the implications of the above model for the management of the stock? We shall look at this in two simplified settings. In one, a constant escapement strategy is followed. This aims at always leaving behind some target level of the stock after fishing every year. In years when the stock is below the target level there is no fishing. Formally, the target escapement rule is:

$$Q = \max(0, S - \overline{S}) , \quad (7)$$

where Q is the permitted catch (total catch quota) and $\overline{S}$ is the target escapement. Under this rule, the catches of fish will vary because the stock varies and all the stock beyond the target level will be taken. The catch per year in a long-term perspective depends on the target level set, and so do the variations in the catch. There might be some trade-off, however, between the catch per year and the variability, measured as standard deviation, maximum versus minimum catch, or the number of years in some given time period without any fishing at all. The high variability of catches under the target escapement strategy is likely to be undesirable, because of the large, but only occasionally utilized, fishing and processing capacity necessary to cope with the occasional peaks in catches.

In the other case, a certain share of the stock is fished every year (constant fishing mortality), except that when the stock is below a critically low level it is left unfished. This critical level is set at 5,000 mt, the level the stock is believed to have been close to during the catch moratorium 1968–86. In this case:

$$Q = \max(0, sS \text{ if } S > 5000) , \quad (8)$$

where s is the rate of exploitation. Under this strategy the catches will vary proportionately with the stock, but they will presumably be less variable than under the target escapement strategy. On the other hand, catching a given proportion of the stock will not spare the stock when it happens to be at a low level (except if it is below the critical level), which might impede a recovery of the stock when it has fallen to a low level. This could lead to a lower average catch than the target escapement strategy and possibly even to a greater variability by impeding stock recovery at low stock levels.

The two strategies are investigated by simulating the stock over a 100-year period, making 100 simulations for each target stock level or fixed exploitation rate. The simulations start with a plentiful stock of 4.0 million mt, close to the level in the early 1930s. Then a value of the random environmental variable is drawn for each year with a random number generator and the stock is updated according to the catch strategy followed. Both the quadratic and the logarithmic model discussed above are examined.

Target Escapement

Under this strategy, the initial stock level is reduced during the first year to the target escapement level, which in most cases produces an unrealistically large initial catch. This initial catch is ignored in calculating the average, maximum, and standard deviation of catches. The catch is set equal to the beginning stock level each year plus the surplus growth less the target stock, or zero otherwise, so ignoring that some fish that are caught would have died within the year for natural reasons.

The results are summarized in Figures 6 and 7. The former shows the average catch per year, the standard deviation of the catch over the 100-year period averaged over the 100 simulations, and the maximum and minimum catch per year obtained in any simulation. Both models produce similar results. The catch per year rises as the escapement level increases up to a level of 1.4 (logarithmic model) or 1.6 (quadratic model) million mt and then the catch stays relatively constant at about 160,000 (logarithmic model) or 200,000 (quadratic model) mt per year. Thereafter it falls off as the

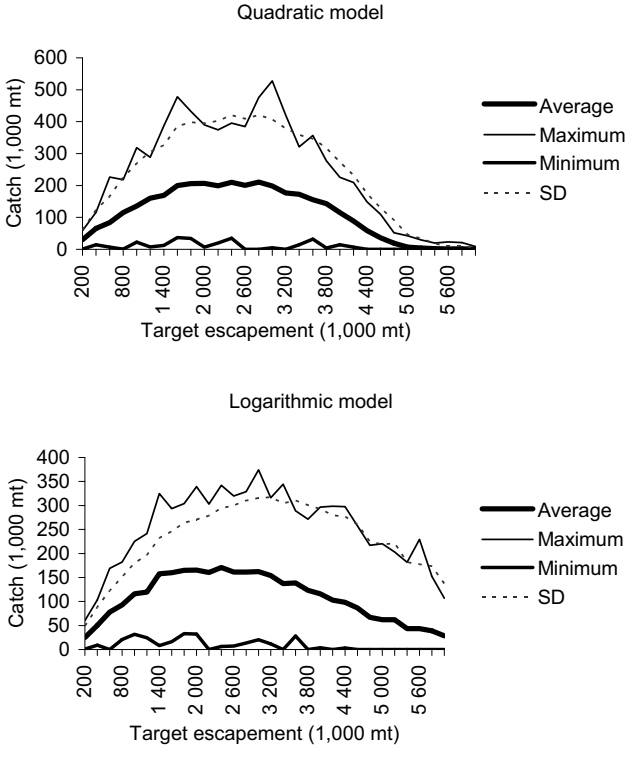

Figure 6: Average, maximum, and minimum catch per year, and standard deviation (SD) of catches as functions of target escapement.

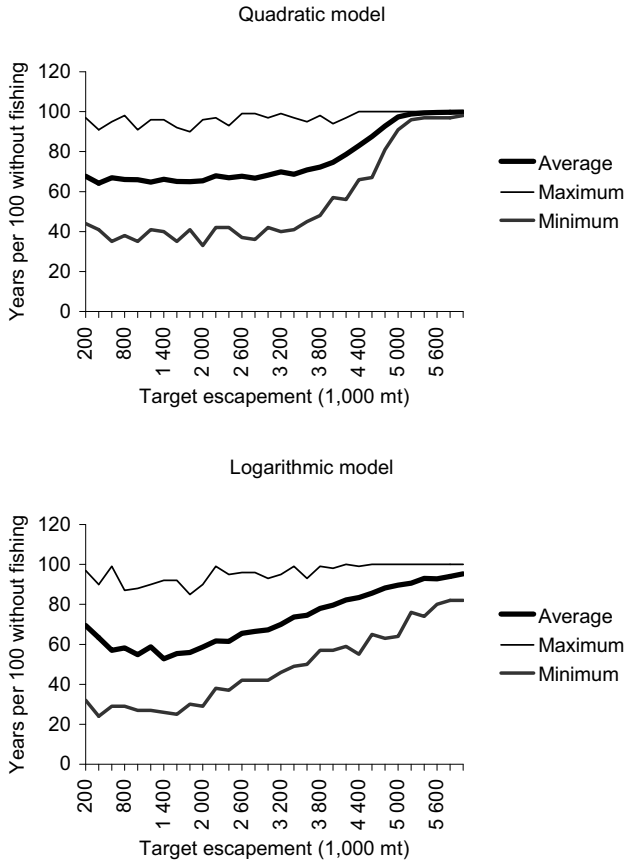

Figure 7: Average, maximum, and minimum number of years (*T*) without fishing as functions of target escapement.

escapement level exceeds 3.0 (quadratic model) or 3.4 (logarithmic model) million mt per year. At an escapement level of 5.0 million mt there is virtually no catch in the quadratic model, but still some in the logarithmic model because of its ability to sustain a large stock with a positive surplus growth where the quadratic model would produce a negative growth. Note that some catches are possible even if the target escapement is set well above the average carrying capacity parameter (K = 3.1 million mt) because of the variability of surplus growth.

The catches are highly variable. The standard deviation, averaged over the 100 simulations, is about as large as the maximum annual catch, especially in the quadratic model. The maximum catch is greater and more variable in the quadratic model, but both models produce a minimum catch quite close to zero for all target escapement levels. This variability is reflected in the number of years without any fishing. The average number of years without any fishing in a 100-year period is fairly constant in the quadratic model, slightly above 60, up to a target escapement level of about 3.0 million mt. After that, it rises gradually until there is hardly ever any fishing as the target escapement level exceeds 5.0 million mt. The minimum number of years without fishing in any 100-year period hovers around 40 years with an escapement level up to 3.4 million mt.

In the logarithmic model, the average number of years without fishing is slightly more variable. Initially it falls as the target escapement level rises and dips below 60 years, and then rises gradually as the target escapement exceeds 2.0 million mt. It takes a higher escapement level than in the quadratic model to reduce the years with fishing to zero. The minimum number of years without fishing in any 100-year period is lower than in the quadratic model, staying between 25 and 30 years until the target escapement exceeds 2.0 million mt. The maximum number of years without fishing in any 100-year period is similar to the quadratic model but somewhat more variable; it can be close to 100 even with target escapement as low as a few hundred thousand metric tons.

There is not really much of a trade-off between catch per year and the variability of catches. In the quadratic model, the catch per year is fairly constant over a range of escapement levels from 1.6 to 3.0 million mt. Both the standard deviation of catches and the average number of years without fishing are also fairly constant over that range. In the logarithmic model, both the standard deviation of catches and the average number of years without fishing continue increasing after the average catch has flattened out. On the basis of this model there would be no point in raising the escapement level beyond 1.4 million mt, when the average catch begins to flatten out.

Constant Exploitation Rate

Let us then turn to the case where a constant share of the stock is caught every year. Figure 8 shows how the average catch per year, the maximum and minimum catch per year, and the standard deviation of catch per year vary with the share of the stock being fished. The average catch peaks for quite a low exploitation rate, approximately 10%, both in the quadratic and the logarithmic model. There is not much difference between the peaks produced by the two models; the quadratic model produces a slightly higher peak, 140,000 mt, while the logarithmic model gives about 130,000 mt. For higher exploitation rates, the average catch per year tapers off rather quickly. It is noteworthy that the maximum catch per year in any simulation peaks at a higher exploitation rate than the average catch per year; it increases steeply to 350,000–400,000 mt for an exploitation rate of 0.15 and then falls quickly[5]. The standard deviation of catches increases with the exploitation rate until the latter reaches 20% and then stays high, tapering off as the exploitation rate exceeds 50%.

[5]In the simulations reported, the exploitation rate was varied in intervals of 0.05.

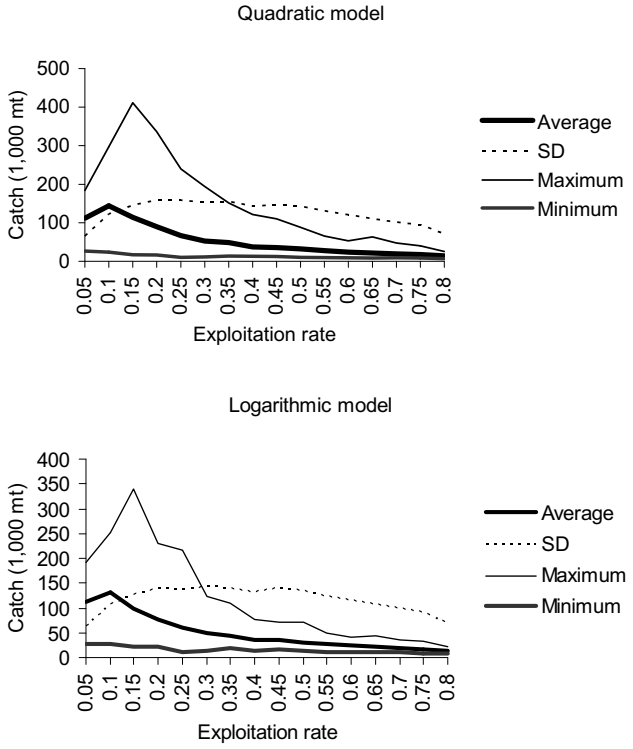

Figure 8: Average, maximum, and minimum catch per year and standard deviation (SD) of catches as functions of the share of the stock caught.

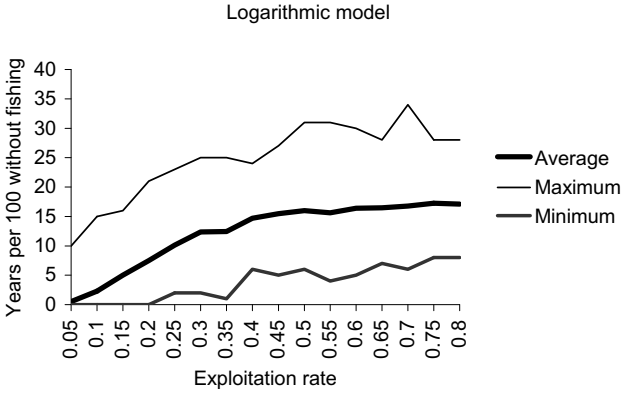

Figure 9: Average, maximum, and minimum number of years (*T*) without fishing as functions of the share of the stock caught.

In the quadratic model, the fishery is hardly ever shut down (recall that this was assumed to happen if the stock fell below 5,000 mt, which is an almost trivially low level). In the logarithmic model, this occurs more frequently (fig. 9). For an exploitation rate of 10%, which produces the maximum average catch per year, this hardly ever happens on the average, or in less than one year out of 100, but the maximum number of years that the fishery could be shut down because of this is 10. The number of shut-down years increases quickly with the exploitation rate, but even with an exploitation rate of 80% the fishery would only be shut down about 17 years on average, while the maximum number of years of shut-down could be around 30.

Comparing the Strategies

The target escapement strategy results in a greater catch per year. This is especially so in the quadratic model, where it produces about 200,000 mt per year on the average, while the constant exploitation rate produces 140,000 mt. In the logarithmic model, target escapement produces 160,000 mt per year on the average, while a constant exploitation rate produces 130,000 mt. But the variability of catches is much greater with the target escapement strategy. The maximum standard deviation is more than twice what it is under the constant exploitation rate: 420,000 mt versus 160,000 mt in the quadratic model, and 310,000 mt versus 140,000 mt in the logarithmic model. The much higher variability of catches under the target escapement strategy is also reflected in more frequent shut-downs; on average the fishery would be closed more than half the time (50–60 years out of 100) under a target escapement strategy that aimed at maximizing the average catch, while this would seldom happen with a constant exploitation rate. Higher yields on average would thus be attained at the expense of more frequent closures.

So, even if the target escapement strategy would yield higher catches per year it is not obviously better than the constant exploitation rate, as it produces a much greater variability in catches and much more frequent fishery closures. It is noteworthy that the exploitation rate that maximizes the average catch is quite low, only 10%, and the target escapement level that maximizes the average annual catch is rather high, 1.4 and 1.6 million mt, depending on which model we use.

These results are rather similar to those reported in the fishery management plan for the coastal pelagic species (PFMC 1998, Appendix B). There it was found that with a constant fishing mortality, the maximum average catch per year would be obtained when $F = 0.12$, resulting in an average annual catch of about 180,000 mt, a standard deviation of 180,000 mt, and no year without any catch. The instantaneous natural mortality of sardines has been estimated at 0.4, so $F = 0.12$ corresponds to an exploitation rate of 9% per year. With our model, we find that an exploitation rate of 10% per year would give a maximum annual catch of 130,000 mt or 140,000 mt, a standard deviation of a little over 100,000 mt, and very few or no years without any fishing at all. In the management plan it was found that a pulse fishery with a target escapement of 1.0 million mt would maximize the average annual catch, providing an average of about 200,000 mt, and result in no fishing about half the time and a standard deviation of catches of about 300,000 mt. In our model, we find that a target escape-

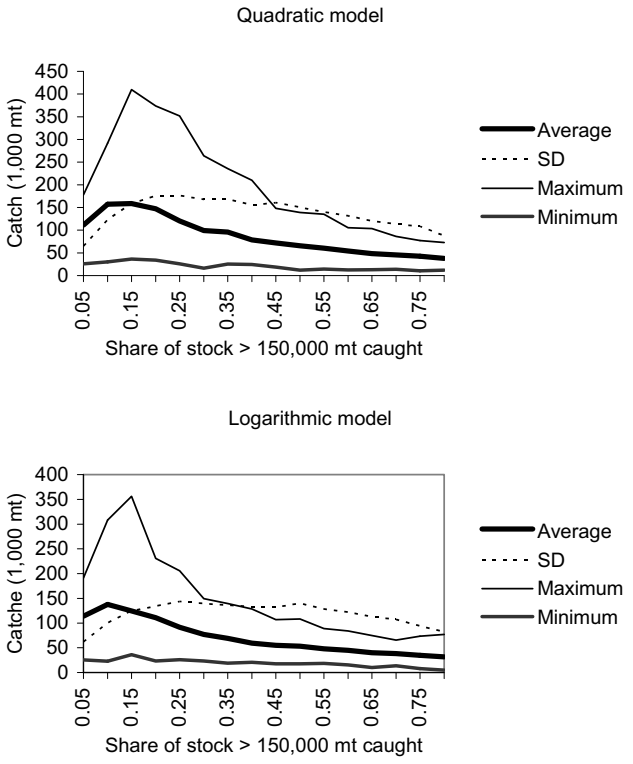

Figure 10: Average, maximum, and minimum catch per year and standard deviation (SD) of catches as functions of the stock share in excess of 150,000 mt caught.

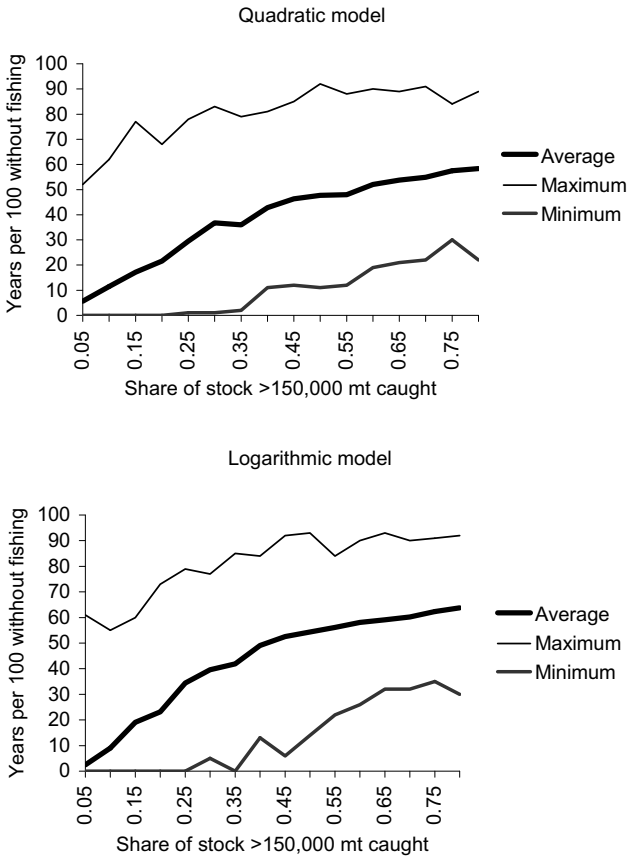

Figure 11: Average, maximum, and minimum number of years (T) without fishing as functions of the share of the stock beyond 150,000 mt caught.

ment of 1.4 or 1.6 million mt would maximize the average annual catch at 160,000 mt or 200,000 mt, but probably result in a closure of the fishery more than half the time and a standard deviation of catches of 230,000 mt or 390,000 mt. Thus, there is clearly a tradeoff between average annual catch and the variability of catches; greater stability and fewer closures of the fishery must be bought for lower catches on the average.

A HYBRID STRATEGY

The current PFMC management strategy employed for the Pacific sardine is a hybrid of the two considered above (PFMC 1998). The total catch quota is set equal to a certain fraction of the stock beyond a target escapement of 150,000 mt, the fraction depending on environmental conditions measured by the average sea surface temperature at the Scripps pier over the last three years. Under the current strategy, the total catch quota is also subject to a maximum allowable catch constraint.

Here we initially consider the hybrid strategy with a constant exploitation rate and then allow the share of the stock beyond 150,000 mt to vary according to the random environmental variable. For comparison with the earlier strategies we do not impose the maximum allowable catch constraint. The catch quota (Q) is:

$$Q = \max\left[0, s\left(S - \overline{S}\right)\right], \qquad (9)$$

where s is the exploitation rate and $\overline{S}$ the target escapement (150,000 mt).

The results (figs. 10 and 11) are not very different from those obtained for the constant exploitation rate above (figs. 8 and 9). The average annual catch is still maximized with an exploitation rate of 10%, although a rate of 15% gives virtually the same average annual catch in the quadratic model. For the quadratic model, the average annual catch is a bit higher in the hybrid strategy, about 160,000 mt compared with just over 140,000 mt in the simple constant exploitation rate strategy. For the logarithmic model, the average annual catch in the hybrid strategy is 137,000 mt, versus 132,000 mt in the simple constant exploitation rate strategy. But the variability is considerably greater. This is reflected primarily through longer period the fishery is shut down and less so through a higher standard deviation of catches. In the quadratic model, the standard deviation of the annual catch is virtually the same in the hybrid strategy as it is for the simple constant exploitation rate strategy at the 10% rate of exploitation, while in the logarithmic model it is slightly higher (107,000 mt versus 100,000 mt). But while in the quadratic model the fishery was

TABLE 3
Results from adjusting the exploitation rate according to environmental conditions. Catches in thousands of metric tons, shut-down time (T) in years out of 100.

	Hybrid, adjustable exploitation rate strategy						Constant exploitation rate strategy	
	k	Average catch	Average T	Average s	Maximum s	Minimum s	Average catch with s = 0.1	Average T with s = 0.1
Quadratic	0.06	185.1	16.8	0.114	0.759	0	143.7	0
Logarithmic	0.04	162.6	9.9	0.105	0.405	0	131.9	2.3

almost never shut down under the simple constant exploitation rate strategy, it is shut down for about 11 years on the average under the hybrid strategy, with the maximum and minimum number of shut-down years being 62 and 0, respectively. In the logarithmic model, the average number of shut-down years is 9.05 for the hybrid strategy compared with 2.29 in the simple constant exploitation rate strategy. The hybrid strategy, thus, is not unambiguously better than the constant exploitation rate strategy; it buys a higher average catch for greater variability in catches and more frequent shut-downs.

As already mentioned, the management strategy currently employed for the sardine stock lets the exploitation rate vary according to environmental conditions. Here we shall mimic this by letting the rate of exploitation deviate from the optimal constant one (s^o) according to the realized value of the environmental variable (U) in two adjacent periods. The catch quota (Q) in Equation 9 above is modified to:

$$Q = \max\left[0, \left(s^o + k\left(\frac{U_{t-1} + U_t}{2}\right)\right)(S_t - \overline{S})\right], \qquad (9')$$

where s^o = 0.1, k is an adjustment factor to be determined so as to maximize the average catch per year, and U is determined by Equation 6 and the random draw of V. The resulting exploitation rate, $s^o + k$, is bound between 0 and 1.

The results are shown in Table 3. The adjustment factor k is sufficiently high for both models to produce quite high maximum exploitation rates (0.759 and 0.405, higher for the quadratic model) and minimum exploitation rates of 0. This is not entirely surprising; the target escapement strategy is the one that maximizes the average annual catch, which implies a quite variable exploitation rate. The average annual catch is raised by 20%–30%, but this comes at the cost of greater variability and having to shut down the fishery 10%–20% of the time on the average. Whereas, with a constant exploitation rate of 0.1, the fishery is hardly ever shut down. So, by adjusting the exploitation according to environmental conditions it would be possible to increase the average annual catch, but at the expense of more variable catches and having to shut down the fishery more often.

CONCLUSION

In this paper, we have used a surplus growth model to analyze the California Pacific sardine fishery. The model is capable of producing crashes in the stock even in the absence of fishing, which has apparently occurred several times in the past. All it takes to produce such crashes is a few unfortunate draws of a random variable reflecting unfavorable conditions in the environment. Once the stock has been knocked down to a very low level it will take a long time to recover because small stocks produce little surplus growth despite favorable environmental conditions. Long recovery periods after crashes could thus be due to this small-stock-little-growth effect rather than prolonged unfavorable environmental regimes.

Maximizing the average annual yield from the stock would entail a fishing strategy which aims at leaving behind a certain target stock (escapement). That this kind of strategy maximizes the returns from a fishery, given a constant price of fish, is long since well established (Reed 1979). But for fluctuating stocks this comes at the cost of highly variable catches; in the sardine case the fishery would be shut down more than half of the time if the policy aims to maximize the average annual catch. This is indeed likely to cause inconvenience for the industry.

Alternatively, one could use a constant rate of exploitation. This would mean less variability of catches, but they would still vary as long as the stock varies. The exploitation rate that would maximize the average annual catch is in fact quite low, only about 10%. The results from our model are in broad agreement with simulations undertaken to determine the optimal harvest policy for sardine in the Pacific Fishery Management Council's Fishery Management Plan for Coastal Pelagic Species (PFMC 1998), which were conducted using a different model; there it was found that the optimal fishing mortality was 0.12, implying an exploitation rate of about 9%. Our model produces an average annual catch that is somewhat lower, 130,000–140,000 mt compared to 180,000 mt. The simulations in the fishery management plan also found that a target escapement policy would maximize the average annual catch, but would shut down the fishery almost half the time. In our model, the fishery is shut down even more frequently, and the

TABLE 4
Comparison of results for four exploitation strategies.
Catches in thousands of metric tons, shut-down time in years out of 100.

	Average catch		Shut-down years	
Strategy	Q-model	Log-model	Q-model	Log-model
Target escapement	210	170	67	61
Constant exploitation rate	144	132	0	2
Hybrid, constant exploitation rate	158	137	11	9
Hybrid, adjustable exploitation rate	185	163	17	10

target escapement that maximizes the average catch per year is greater.

The currently employed harvest control strategy in the sardine fishery is a hybrid strategy, with a low (150,000 mt) target escapement, an exploitation rate that adjusts according to the ocean temperature at the Scripps pier for the last three years, and a maximum allowable catch constraint. Our model shows that such a hybrid strategy can indeed increase the average annual catch (without exceeding the current maximum allowable catch: 200,000 mt), but at the cost of greater variability, again manifested in more frequent shut-downs. Varying the exploitation rate according to environmental conditions increases the average annual yield still further, but also increases the variability in catches and results in more frequent fishery closures. Table 4 compares the results of the four strategies considered.

The target escapement harvesting strategy, the constant exploitation rate strategy, and the hybrid strategy could all be implemented through individual fishing quotas, which could be transferable or not. Whichever of these strategies is applied, the total catch quota would be set on the basis of stock assessment. With the target escapement strategy the total allowable catch would be set as the difference between the assessed stock level and the escapement level, while with the constant exploitation rate strategy it would be set as a prescribed share of the assessed stock. Since stock assessment is often inaccurate and can be improved as more is learned about the stock during the fishing season, it could be advisable to allow for revisions of the total allowable catch as the fishing season progresses. In some other fisheries the management authorities have been compelled to revise their quota prescriptions during the fishing period, usually downwards.

Individual quotas could be determined as fixed shares of the total allowable catch. Under this arrangement, which is the one usually applied in countries where fisheries are regulated with individual transferable quotas, the industry bears all the risk associated with the variability of the fish stock. As the variability in the total allowable catch, as well as the frequency of fishery closures, depends critically on the choice of harvest policy (exemplified here by the target escapement, constant exploitation rate, and the hybrid harvesting strategies), it is only reasonable that the industry has a say, perhaps a decisive say, in what rule is applied. That said, there are clearly aspects of the management of the sardine stock that lie beyond the purview of the industry, especially such as have to do with the importance of the sardine as a source of food for other species.

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MODELING DISPERSAL OF CLONING ECHINODERM LARVAE WITH A GAUSSIAN DISTRIBUTION: FOREVER YOUNG?

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ABSTRACT

Echinoderm larvae clone (reproduce asexually), but the implications of this remarkable life history trait for larval dispersal have not been explored. We develop a simple model of larval dispersal, in which cloning can be incorporated into the numerator of the Gaussian distribution:

$$P(x,t) = \frac{1}{2\sqrt{\pi Dt}}\, e^{\frac{-x^2}{4Dt}} .$$

Each cloning event resets the time to final settlement. The timing of cloning and the number of sequential cloning events influence the dispersal distance, but neither the percent of larvae that clone nor larval mortality has an impact on distance traveled. The percent of larvae that clone and survive control the *number* (probability density) of larvae. The second moment (variance) in the model shows that the "spread" of the dispersion is linearly related to time ($2Dt$), where the constant D is the *diffusivity*. We discuss the implications of a few clones traveling long distances. This may effectively homogenize the population genetics and facilitate invasions but may not affect fishery management. The life history feature of larval cloning results in a limitless larval period (assuming they survive) and may act to promote long distance dispersal of a few larvae.

INTRODUCTION

Asexual reproduction in larval echinoderms was discovered recently (Bosch 1988; Bosch et al. 1989), yet its implications for larval dispersal has not been explored. Knowing how far larvae disperse (see review, Levin 2006) is critical in ecology and is fundamental to our understanding of population and community dynamics. The degree to which marine populations are open or closed (Cowen et al. 2000; Warner and Cowen 2002) is an important area of research. Larval dispersal distances, for example, can be estimated and used to design networks of marine protected areas (Roberts 1997) and to predict species invasions (Neubert and Caswell 2000). Gaussian distributions are often used to model animal dispersal (Okubo and Levin 2001) but have not been used, to our knowledge, to explore the consequences of cloning for dispersing larvae.

Cloning, or larval budding, by planktotrophic bipinnaria larvae of the sea star, *Luidia* spp., has been observed in field-caught specimens (Bosch 1988; Bosch et al. 1989). Larval cloning is quite common with 10%–90% of larvae in the field-caught samples having modified larval arms consistent with cloning (Bosch et al. 1989; Knott et al. 2003). High food concentrations and optimal temperatures appear to promote cloning in the laboratory (Vickery and McClintock 2000) as does the presence of predators (fish mucus) (Vaughn and Strathmann 2008). In addition, clones may themselves clone (Balser 1998; Vickery and McClintock 2000). Cloning asteroid larvae have been collected in several regions in the tropical and subtropical western Atlantic Ocean (Jaeckle 1994), the Sargasso Sea (Bosch et al. 1989), and the Bay of Bengal (Rao et al. 1993). The widespread distribution of sea star clones in the open waters of the oligotrophic western North Atlantic Ocean may be facilitated by the presence of symbiotic bacteria, a potential food source (Bosch 1992).

Purple sea urchins, *Strongylocentrotus purpuratus*, have been a model study organism in developmental biology for more than 100 years, however cloning has only recently been observed (Eaves and Palmer 2003). This oversight is even more egregious when we consider that Mortensen (1921) reported unusual looking brittle star larvae and suggested that they might be clones arising from asexual reproduction. His reports remained unexplored for the next 75 years (Mladenov and Burke 1994; Balser 1998). Cloning has now been observed in all echinoderm classes, with the possible exception of the crinoids (Eaves and Palmer 2003; Rogers-Bennett 2007). Cloning may therefore be an ancestral life history trait within the echinoderms. Lacalli (2000) and Eaves and Palmer (2003) suggest that this trait may be ancestral, possibly even within the deuterostomes which include echinoderms, acorn worms, sea squirts, and vertebrates.

Despite the potential disadvantages encountered with a longer larval period (Strathmann 1974), such as increased mortality by predation (Rumrill 1990) or starvation (Olson and Olson 1989), there are examples of

successful long-lived marine invertebrate larvae (Scheltema 1971; Rice 1981). One mollusk, *Fusitriton oregonensis*, has been observed to settle successfully after 4.5 years in the larval planktonic stage (Strathmann and Strathmann 2007). Larvae can also delay metamorphosis (see review, Pechenik 1990). It has even been suggested that there may be an entirely pelagic bauplan (Eaves and Palmer 2003), although most animals metamorphose at some point. While we do not know the chances of survival of long-lived larvae and larvae that clone, they do have the potential to disperse long distances.

Here we model echinoderm larval dispersal using a Gaussian distribution and compare the dispersal distances in models with and without cloning. We incorporate cloning by having larvae clone at some time t, before settlement, in one pulse, essentially restarting the clock to settlement. The second cloned distribution is the same as the original dispersal pattern (of the *primary* larvae) but has wider dispersion than the original would have had. In this way, we explore the impacts of cloning on dispersal distances traveled by larvae in the model with effects of (1) the time that cloning occurs (early or late larval stage), (2) the percent of larvae that clone, and (3) the influence of multiple cloning events. We discuss the population implications of having a few clones successfully settle and eventually reproduce in distant regions far from the benthic populations where the primary larvae were produced.

THEORY

Suppose a particle (lattice point) moves in a one-dimensional space along the x axis with a most probable displacement Δx in time Δt, and that the particle is observed at regular intervals which are also Δt. If the particle is found at location x relative to an origin $x = 0$ at time t, $+ \Delta t$, one does not know how it got there. It may have arrived at x by moving $-\Delta x$ toward the origin from a larger value of x or by moving Δx away from the origin. For random motion, the two probabilities are equal:

$$P(x_t + \Delta x \mid x_{t+\Delta t}) = P(x_t - \Delta x \mid x_{t+\Delta t}), \quad (1)$$

and

$$P_{total}(x,t) = P(x_t + \Delta x \mid x_{t+\Delta t}) + P(x_t - \Delta x \mid x_{t+\Delta t}). \quad (2)$$

The notation means that, having observed a particle at location x at time $t + \Delta t$, the probability that it was at $x + \Delta x$ is equal to the probability that it was at $x - \Delta x$ at time t. Since there are no other possible observations, the sum of these two probabilities is the total probability $P_{total}(x,t)$, which is usually normalized to 1.0.

The equation $y = f(x + at) + g(x - at)$ has a long history and a variety of names. In this restricted form, it is called the d'Alembert equation (Wylie and Barrett 1982). One way of treating it is through a Taylor expansion (Appendix) to arrive at:

$$\frac{\partial P(x,t)}{\partial t} = D \frac{\partial^2 P(x,t)}{\partial x^2}, \quad (3)$$

where the constant D is called the *diffusivity* (Okubo and Levin 2001). This is a *parabolic equation*, one of three classes of d'Alembert equations, and its solution is well known (Appendix):

$$P(x,t) = \frac{1}{2\sqrt{\pi D t}} e^{\frac{-x^2}{4Dt}}. \quad (4)$$

The function $P(x,t)$ is assumed to be separable and can be treated as $P(x)$ at fixed t over the range $[-\infty,\infty]$ of x. $P(x)$ at fixed t is used to generate Figures 1 and 2. $P(x)$ at fixed t is an even function over symmetrical intervals in x, so it has a first moment (mean) of zero. It is the second moment $M_2(t)$ that is of interest:

$$M_2(t) = \int_{-\infty}^{\infty} x^2 P(x,t)\,dx\,`. \quad (5)$$

This can be integrated by parts twice (Appendix) to give:

$$M_2(t) = 2D \int_{-\infty}^{\infty} P(x,t)\,dx, \quad (6)$$

but the integral of the probability over all event space $\int_{-\infty}^{\infty} P(x,t)\,dx$ is 1.0, so $M_2(t) = 2D$. Taking the second moment (variance) over the interval $[0,t]$ from a time defined as zero to a finite time t, gives:

$$M_2(t) = 2Dt. \quad (7)$$

Hence, the variance (spread of the probability density function) is *linear* with time. The lower limiting case is that of a particle observed at $t = 0$ which has not moved away from the origin. The upper limiting case is that of $M_2(t) \to \infty$ as $t \to \infty$. This is the case of complete uncertainty as to the location of the particle. The probability of finding a particle becomes very small at large x but it does not become zero.

A DISPERSION MODEL

A population P of echinoderm larvae diffuses away from a pulse at an origin $x = 0$ so as to give a Gaussian or some similar distribution. (The argument does not depend on the details of the dispersion model.) The distance away from the origin, $x = f(t)$ is determined by the diffusion speed v and the time in transit t. The larvae can move in two or three dimensions, so distance x and velocity v are vectors in x, y, z space. We consider only one dimension for simplicity.

Dispersion of larvae in the absence of cloning is modeled in Figure 1 as a Gaussian distribution. The horizontal axis represents the distance traveled by larvae in a specific time $x = vt$. For illustrative purposes, curves in

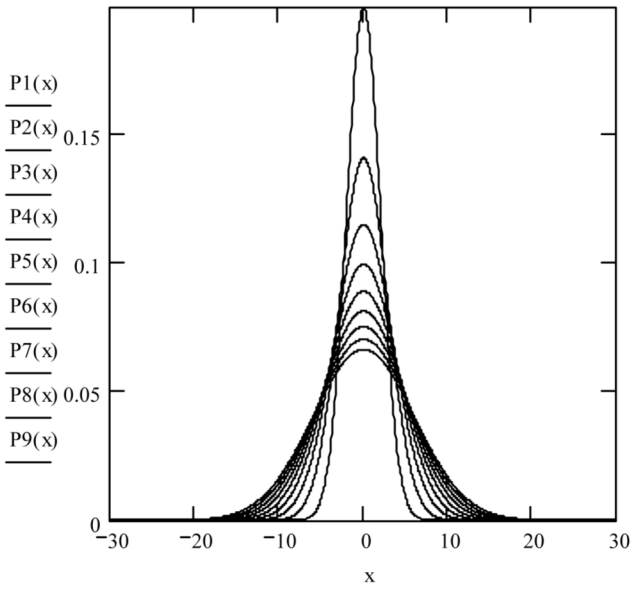

Figure 1. Larval Dispersion as a Function of Time. The horizontal axis is the linear distance away from an origin at $x = 0$. The vertical axis represents a set of number density curves P_1–P_8 of larvae, and time is on the axis orthogonal to x and P. Eight curves are shown at times t_1–t_8. The time axis is truncated at t_8 by settlement.*

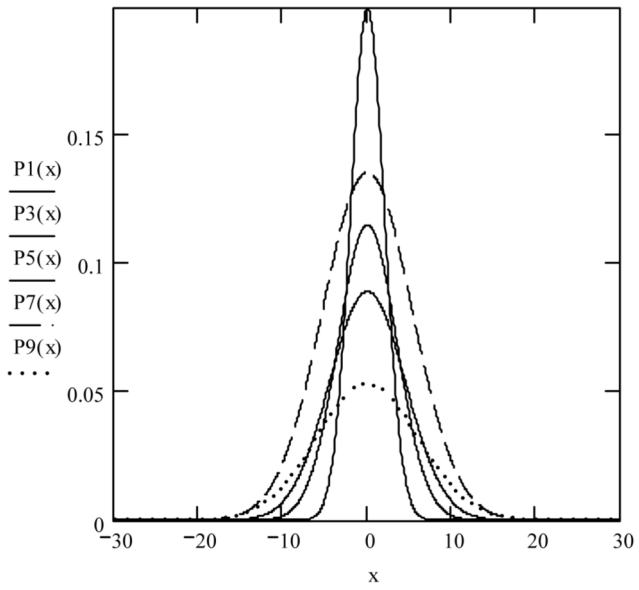

Figure 2. A Continuation of the Model in Figure 1. The curves show cloning at t_7 and settlement of the primary population at t_9. The red (dashed) curve is after 80% cloning but before settlement of the primary population. The blue (dotted) curve is after cloning and settlement. The curves show a decrease in the total number of larvae but an increase in dispersion.

Figure 1 are shown at a sequence of times t_1–t_8. The initial egg distribution t_0 has a high density and is represented by a narrow distribution, essentially a vertical plane of $x = 0$. Assuming 100% survival, the area under the curves is constant but the variance increases with time (as does distance traveled).

Dispersion Model with Cloning

Suppose a certain percent of the larvae cloned in a single pulse at some time t before settling at, say, t_7. The cloning event can be represented by multiplying Equation 4 by an appropriate constant, say, 1.8 for 80% of the larvae cloning. A new diffusion curve is produced with the characteristics of the old curve but with an area that is larger than the area before cloning. In addition to the population increment, the "clock" is reset (time to settlement is reset) for the new sample of larvae which diffuse until *they* settle, yielding a broader dispersion than the primary larvae would have attained. After settlement of the primary population (the original 100%), the area under the distribution curve is adjusted downward to reflect their loss from the plankton (post settlement). We make a few simplifying assumptions: (1) the absence of distance-dependent mortality, and (2) pulse cloning (no distribution of cloning over time).

Figure 2 shows the results of a cloning event at t_7. The area of the Gaussian is increased by an amount depending on the number of clones produced, say 80% of the original population. The new population, composed of cloned larvae, is distributed over the same standard deviation and variance as the initial population at the time of cloning, but the variance continues to increase as these larvae disperse. The density curve after cloning, but before settlement of the primary population, is shown as curve P_7 in Figure 2. The distance traveled by the clones increases in the model. Cloning occurring at times closer to settlement (late larvae) enhances dispersion relative to early cloning.

At some point the primary population settles and the area under the distribution curve drops to 80% (the percent of clones). The cloned population, however, continues to disperse and its variance, and thus its distribution, continues to increase.

Multiple Cloning Events

This argument can be continued *ad infinitum* since clones can continue to clone (Balser 1998), resulting in long distance dispersion of a few larvae. After four generations the gain in dispersal is substantial. The density of individuals reaching the fourth generation at 80% cloning is reduced to $0.8^4 = 0.41$ of the original population. Although the larval population (ignoring mortality) is reduced by more than half after four cloned generations, the original larval population may have been very large (e.g., one female laying several million eggs).

Mortality and Currents

In the ocean, additional factors influence dispersal, such as mortality and currents. These factors can be incorporated into the model in simple ways that will not

*Online version of article has figures in color.

change the shape of the dispersal patterns or the general conclusions. Mortality will diminish the height of the curve (number density) and currents will shift the curve along the distance axis "downstream" or "upstream." Mortality can be incorporated into the model by simply multiplying the numerator by a mortality rate (either constant or variable). Similarly, currents can be included as a constant, either positive or negative, added to the right side of the equation.

DISCUSSION

Dispersal distances of larvae and their clones in simple Gaussian dispersal models increase linearly with time ($2Dt$) as seen in the second moment of the Gaussian model. Several variables influence the time larvae spend in the dispersal stage, including (1) the timing of cloning (early or late stage), and (2) the number of cloning events. Both increase dispersal, while the percent of clones does not. Cloning of late-stage larvae increases the time in the plankton more than cloning of early larvae does. Furthermore, if cloning increases developmental time for primary "parent" larvae and they metamorphose, as might occur when cloning occurs by fission, this too will increase the time in the plankton and therefore dispersal.

In our model, populations with multiple cloning events traveled the greatest distances since we assume each cloning event resets that population's larval dispersal clock. It is noteworthy that a linear combination of Gaussian, which enables us to extend our model for multiple cloning events and to construct a curve with a "fat tail" as in the Weibull equation (Weibull 1951; Greene 2004). In our model, any cloning mechanism which increases the developmental time of either the primary larvae or the clone will lead to further dispersal. This suggests that factors which increase time in the plankton warrant further research, specifically, (1) the timing of cloning (early or late larval stage), and (2) the number of times that an individual clones, both in the laboratory and in the field.

There are planktonic larvae that are long-lived and these larvae have been coined "teleplanic" larvae, or far wandering (Scheltema 1971). Sipunculid larvae, for example, have been found in the vast majority of open ocean plankton samples and it is estimated they may be planktonic for three to eight months, possibly traversing ocean basins (Rice 1981). Clearly, planktotrophic larvae, with the ability to clone, are capable of teleplanic dispersal. Cloning differs from delayed metamorphosis in that delays are for a limited time period and have negative consequences for some lecithotrophic larvae (Pechenik 1990; Pechenik et al. 1998). Cloning, on the other hand, does not appear to be inherently "bad" for larvae. Cloning might have negative consequences if clones result in a smaller initial size leading to a smaller size at metamorphosis, as has been shown for non-cloning larvae when initial egg size was experimentally reduced (Hart 1995).

Cloning, in addition to increasing the time spent in the dispersal stage, also increases the number of larvae. Increasing the number of larvae by cloning (which may increase the numbers surviving) simply increases the height of the dispersion curve but has no immediate impact on the distance traveled. The width of the curve "flattens out" over time *but the variance increases without limit*. Several factors that appear at first glance to conflict with this conclusion turn out to be unimportant; among them is larval mortality. Larval mortality does not influence the time-dependent variation of the dispersion though it does influence the *number* (probability density) measured near point x at some time t.

The ability of echinoderms to clone as larvae prior to settlement coupled with the production of tens of millions of eggs renders assumed limits of dispersion distances based on the time to settlement untenable. Even if some of the assumptions used in the present model, specifically the Gaussian dispersion curve, or pulse cloning, are not met, a limit on *dispersal distance by larval period* is incorrect. For echinoderms, larval "transport envelopes," regions within which they may disperse, as for coral reef fishes (Roberts 1997), either have leaky borders or can not be established. Similarly, species with secondary settlement, such as mussels (Bayne 1964), may not be retained locally since newly settled juveniles may disperse a "second" time, rendering the identification of dispersal windows (envelopes) challenging. The life history feature of cloning may act as an opposing force to factors which promote local retention (Swearer et al. 1999; Marko et al. 2007).

The ability of a few clones to travel long distances has implications for the population genetics of echinoderms. A few individuals traveling long distances may effectively homogenize the genetics at distant locations such that there is little or reduced differentiation in recruits relative to adults as has been observed (Flowers et al. 2002). In addition, cloning is a clear violation of Hardy-Weinberg assumptions of random mating (B. Swalla pers. comm.). A few individuals can serve as "founders," establishing new populations of invasive species far from the source (Carlton 1989), or can colonize empty patches. Dispersal of clones, however, may complicate the design of marine reserve networks (Shanks et al. 2003). While a few individuals may be capable of modifying the genetics and/or establishing new populations, we do not envision that a few clones may provide a "rescue effect" for fished areas or influence fishery management. Long distance "spillover" from marine protected areas is likely to be negligible from a fishery perspective. In the model,

only a few clones traveled long distances as seen by the low profile and very long tail of the distribution curve.

The results of our model show that the addition of cloning greatly enhances long-distance dispersal. While modeling larval dispersal as a Gaussian distribution is not new (Okubo 1971; Possingham and Roughgarden 1990; Okubo and Levin 2001), the incorporation of asexual larval reproduction is. Theoretically, the distance traveled is unlimited if there are no limits to cloning events, rendering the larval period indefinite and making the larvae potentially immortal. However, dispersal would not be related to time in the plankton for demersal larvae (Gerrodette 1981).

In our Gaussian model, which assumes Fickian diffusion with a constant *D* diffusivity, dispersal distance is linearly related to time. In comparison with data on the dispersal of dye in the ocean, the variance (the second moment) was found to increase faster than linearly such that time was to the 2.34 power (Okubo 1971), suggesting that dispersal of surface currents in the ocean may be greater than our model depicts. Nevertheless, Gaussian curves are being used to track kelp spore dispersal patterns particularly for long-distance (3–12,000 m) dispersal incorporating current information (Gaylord et al. 2006). Dispersal models such as the ones presented here can help focus research questions on the dispersal biology of larval cloning which, in turn, influences population dynamics, population genetics, invasion biology, and marine protected area design.

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APPENDIX

S1. The Diffusion Equation

The *master equation* describing the one-dimensional random motion of lattice points (see text) situated at a distance Δx apart is:

$$P(x,t+\Delta t) = \frac{1}{2}\,P(x-\Delta x,t) + \frac{1}{2}\,P(x+\Delta x,t)\ . \quad \text{(S.1)}$$

Taylor expansion (de Vries et al. 2006) of each term gives:

$$P(x,t) + \Delta t\ \frac{\partial P(x,t)}{\partial t} + \frac{(\Delta t)^2}{2}\,\frac{\partial^2 P(x,t)}{\partial t^2} + \ \cdots$$

$$= \frac{1}{2}\left[P(x,t) - \Delta x\ \frac{\partial P(x,t)}{\partial x} + \frac{(\Delta x)^2}{2}\ \frac{\partial^2 P(x,t)}{\partial x^2} + \cdots + \right.$$

$$\left. P(x,t) + \Delta x\,\frac{\partial P(x,t)}{\partial x} + \frac{(\Delta x)^2}{2}\,\frac{\partial^2 P(x,t)}{\partial x^2} + \ \cdots \right].$$

We retain only the first three terms of each expansion. A good deal of cancellation takes place. The first term in each expansion $P(x,t)$ appears on both sides of the equation and drops out. The second terms of the expansions lead to:

$$\Delta t\,\frac{\partial P(x,t)}{\partial t} = \frac{1}{2}\left[-\Delta x\,\frac{\partial P(x,t)}{\partial x} + \Delta x\ \frac{\partial P(x,t)}{\partial x} \right],$$

where the terms on the right cancel. The third terms give:

$$\frac{\Delta t}{2}\ \frac{\partial^2 P(x,t)}{\partial t^2} = \frac{1}{2}\ \frac{(\Delta x)^2}{\Delta t}\ \frac{\partial^2 P(x,t)}{\partial x^2}\ ,$$

where both sides have been divided by Δt. Assembling all residual terms, we have:

$$\frac{\partial P(x,t)}{\partial t} + \frac{\Delta t}{2}\ \frac{\partial^2 P(x,t)}{\partial t^2} = \frac{(\Delta x)^2}{2\Delta t}\ \frac{\partial^2 P(x,t)}{\partial x^2}\ . \quad \text{(S.2)}$$

The second term on the left drops out as $\Delta t \to 0$ and the pre-multiplier on the right

$$\frac{(\Delta x)^2}{2\Delta t}$$

in the limit of $\Delta x,\ \Delta t \to 0$ approaches a constant D which is called the *diffusion constant D* from Fick's second law (Crothers and Eisenberg 1979), or the *diffusivity*. This leaves:

$$\frac{\partial P(x,t)}{\partial t} = D\ \frac{\partial^2 P(x,t)}{\partial x^2}\ . \quad \text{(S.3)}$$

S.2 Separation of the Partial Differential Diffusion Equation

The parabolic partial differential equation

$$\frac{\partial P(x,t)}{\partial t} = D\ \frac{\partial^2 P(x,t)}{\partial x^2}$$

can be reduced to two ordinary differential equations by making the simplifying assumption that the solution $P(x,t)$ is the product of a function in x only and a function in t only, $P(x,t) = p(x)p(t)$. This substitution gives:

$$\frac{\partial p(t)}{\partial t}\ p(x) = D\ \frac{\partial^2 p(x)}{\partial x^2}\ p(t), \quad \text{(S.4)}$$

which, when divided by $p(x)p(t)$ gives:

$$\frac{1}{p(t)}\ \frac{\partial p(t)}{\partial t} = D\ \frac{1}{p(x)}\ \frac{\partial^2 p(x)}{\partial x^2}\ .$$

The left side of this equation is a function of the independent variable t and the right side is a function of the independent variable x. If we evaluate each side of the equation with arbitrary values of x or t, the two sides might be equal by luck, but they would not be *identically* equal. The only way for them to be identically equal is for each side to be equal to a constant. Call the constant $-\lambda$. Now:

$$\frac{1}{p(t)}\ \frac{dp(t)}{dt} = -\lambda\ , \quad \text{(S.5a)}$$

and

$$D \frac{1}{p(x)} \frac{d^2p(x)}{dx^2} = -\lambda . \quad \text{(S.5b)}$$

S.3 Solution of the Time-Dependent Equation

Equation S.5a can be written:

$$\frac{dp(t)}{p(t)} = -\lambda\, dt . \quad \text{(S.6)}$$

When integrated, we get:

$$\ln p(t) = -\lambda t + C = -\lambda(t - t_0) = -\lambda t , \quad \text{(S.7)}$$

for $t_0 = 0$, or, equivalently:

$$p(t) = e^{-\lambda t} . \quad \text{(S.8)}$$

The logarithmic decrease in $p(t)$ in Eq. S.7 can be seen by following the peak probability from t_0 to t_8 in Figure 1. One can see from Eq. S.8 why the separation constant was chosen as $-\lambda$ rather than λ. Choosing λ leads to an exponential *increase* in $p(t)$, which is contrary to the physical reality of the problem.

S.4 The Second Moment

The diffusion equation:

$$\frac{\partial P(x,t)}{\partial t} = D \frac{\partial^2 P(x,t)}{\partial x^2} , \quad \text{(S.3)}$$

has a first moment (the limiting sum of deviations about an arithmetic mean):

$$\mathrm{M}_1(t) = \int_{-\infty}^{\infty} x P(x,t)\, dx , \quad \text{(S.9)}$$

and a second moment (the variance about the mean):

$$\mathrm{M}_2(t) = \int_{-\infty}^{\infty} x^2 P(x,t)\, dx . \quad \text{(S.10)}$$

The left-hand side of the diffusion equation is a time derivative:

$$\dot{\mathrm{M}}_2(t) = \int_{-\infty}^{\infty} x^2 \frac{\partial P(x,t)}{\partial t}\, dx , \quad \text{(S.11)}$$

thus it is also true that:

$$\dot{\mathrm{M}}_2(t) = \int_{-\infty}^{\infty} x^2 D \frac{\partial^2 P(x,t)}{\partial x^2}\, dx , \quad \text{(S.12)}$$

which is a space derivative. Notice that we have gotten rid of ∂t in the integral. This is in effect, a separation of variables. The integral in x is vulnerable to the "integration by parts" technique. Since we are dealing with the space part of the equation, we can simplify the notation and let $P(x,t) = P$. Also a common notational simplification is to let

$\frac{\partial P(x,t)}{\partial x} = P_x$ and $\frac{\partial^2 P(x,t)}{\partial x^2} = P_{xx}$. Now:

$$\dot{\mathrm{M}}_2(t) = \int_{-\infty}^{\infty} x^2 D P_{xx} dx . \quad \text{(S.13)}$$

S.5 Integration by Parts

The method has never been better or more succinctly stated than by J. W. Mellor in the early 20th century (Mellor 1929):

The differentiation of the product uv, furnishes

$d(uv) = vdu + udv$

By integrating both sides of this expression we obtain

$uv = \int vdu + \int udv$

Hence, by a transposition of terms, we have

$\int udv = uv - \int vdu + C$

that is to say, the integral of udv can be obtained provided vdu can be integrated.

The constant of integration at the lower limit is subtracted from the constant of integration at the upper limit, so it vanishes.

S.6 Integrating the Space Part of the Moment

To integrate by parts, let $u = x^2$, hence $du = 2xdx$. Also let $v = P_x$ and $dv = P_{xx}dx$. Now $uv = x^2P_x$ and $vdu = P_x 2xdx$. The integral:

$$\int udv = uv - \int vdu + C$$

becomes

$$\int_{-\infty}^{\infty} x^2 P_{xx} dx = x^2 P_x \Big|_{-\infty}^{\infty} - \int_{-\infty}^{\infty} P_x 2x dx , \quad \text{(S.14)}$$

where we have set the limits $[-\infty,\infty]$ to cover the entire probability space. This also gets rid of the constant of integration. The interval is symmetrical about zero and P_x is an odd function over this interval, hence x^2P_x is also odd, $x^2P_x\big|_{-\infty}^{\infty}$ is zero and drops out. An odd function has opposite and equal values at the left and right of the symmetry. Symmetrical integrals of an odd function vanish. An example is $y = x$. The first derivative of the Gaussian is odd about the mean because it is positive to the peak and equal and opposite thereafter. We have reduced P_{xx} to P_x. For this reason Mellor (1929) refers to integration by parts as a *reduction equation*.

We now have the integral $-\int_{-\infty}^{\infty} P_x 2x dx$ to evaluate, but we can do this by repeating the method already used. Integrating by parts again, we get:

$$-\int_{-\infty}^{\infty} P_x 2x dx = -2xP\Big|_{-\infty}^{\infty} + \int_{-\infty}^{\infty} 2DP dx\,. \qquad \text{(S.15)}$$

Now x is odd so $-2xP\big|_{-\infty}^{\infty}$ drops out leaving $\int_{-\infty}^{\infty} 2DP dx$ but this is only $2D\int_{-\infty}^{\infty} P dx$ where, restoring the original notation, the integral $\int_{-\infty}^{\infty} P dx = \int_{-\infty}^{\infty} P(x,t)dx$ is defined as 1.0:

$$\dot{M}_2(t) = 2D\int_{-\infty}^{\infty} P(x,t)dx = 2D\,. \qquad \text{(S.16)}$$

We have the solution over the interval $[-\infty,\infty]$ but we are only interested in one half of it, the interval $[0,\infty]$. Over this interval, the time part of the equation gives:

$$\dot{M}_2(t) = \frac{dM_2}{dt} = 2D\,, \qquad \text{(S.17)}$$

so that $\int_0^t d\mathrm{M}_2(t) = 2D\int_0^t dt$, and

$$\mathrm{M}_2(t) = 2Dt\,. \qquad \text{(S.18)}$$

That is, the position uncertainty or probability dispersion is *linear* with time.

S.7 Solution to the Space-Dependent Part

For the space part of the original equation, Jordan and Smith (1997) define the *variance* as:

$$\sigma^2 = \int_{-\infty}^{\infty} (x-\mu)^2 f(x)dx\,, \qquad \text{(S.19)}$$

where μ is the arithmetic mean and $f(x)$ is some distribution function (see also Eq. S.10). In the *normal distribution* about a mean, $\mu = 0$, and

$$f(x) = \frac{1}{\sigma\sqrt{2\pi}}\, e^{-\frac{x^2}{2\sigma^2}}\,. \qquad \text{(S.20)}$$

The *coefficient of variation* (de Vries et al. 2006) of a one-step random walk is

$$\sigma = \sqrt{\sigma^2} = \sqrt{2Dt}$$

by Eq. S. 18. Substituting for σ yields the desired spatial probability function:

$$f(x) = P(x,t) = p(x)p(t) = \frac{1}{2\sqrt{D\pi t}}\, e^{\frac{-x^2}{4Dt}}\,, \qquad \text{(S.21)}$$

which is the function plotted in Figs. 1 and 2 at sequential fixed values of t (see also Eq. S.7).

S.8 Mathcad Input

One can demonstrate by Mathcad© that all Gaussians in Figure 1

$$\mathrm{P(x)} := \frac{1}{2\sqrt{\pi Dt}}\, e^{\frac{-x^2}{4\cdot Dt}}$$

are normalized to 1.0. For example, at t held constant at 6 time units, the integral over the interval $[-\infty,\infty]$ is:

$$\mathrm{D} := 2 \quad \mathrm{t} := 6$$

$$\int_{-\infty}^{\infty} \left(\frac{1}{2\sqrt{\pi Dt}}\, e^{\frac{-x^2}{4\cdot Dt}} \right)$$

Typical input expressions for Mathcad© are given below. In each case, the time is inserted into the equation as a constant 1, 2, . . . , 9, and the constant D is initially defined as 2 for all.

TABLE S.1
Input Equations for the Mathcad© Two-Dimensional Graphing Function.

$$\mathrm{D} := 2$$

$$\mathrm{P1(x)} := \frac{1}{2\sqrt{\mathrm{D}\pi}}\, \mathrm{e}^{\frac{-x^2}{4\mathrm{D}}} \qquad \mathrm{P2(x)} := \frac{1}{2\sqrt{2\mathrm{D}\pi}}\, \mathrm{e}^{\frac{-x^2}{4\mathrm{D}\cdot 2}} \qquad \mathrm{P3(x)} := \frac{1}{2\sqrt{3\mathrm{D}\pi}}\, \mathrm{e}^{\frac{-x^2}{4\mathrm{D}\cdot 3}}$$

$$\mathrm{P4(x)} := \frac{1}{2\sqrt{4\mathrm{D}\pi}}\, \mathrm{e}^{\frac{-x^2}{4\mathrm{D}\cdot 4}} \qquad \mathrm{P5(x)} := \frac{1}{2\sqrt{5\mathrm{D}\pi}}\, \mathrm{e}^{\frac{-x^2}{4\cdot\mathrm{D}\cdot 5}} \qquad \mathrm{P6(x)} := \frac{1}{2\sqrt{6\mathrm{D}\pi}}\, \mathrm{e}^{\frac{-x^2}{4\cdot\mathrm{D}\cdot 6}}$$

$$\mathrm{P7(x)} := \frac{1.8}{2\sqrt{7\mathrm{D}\pi}}\, \mathrm{e}^{\frac{-x^2}{4\cdot\mathrm{D}\cdot 7}} \qquad \mathrm{P8(x)} := \frac{1.8}{2\sqrt{8\mathrm{D}\pi}}\, \mathrm{e}^{\frac{-x^2}{4\cdot\mathrm{D}\cdot 8}} \qquad \mathrm{P9(x)} := \frac{.8}{2\sqrt{9\mathrm{D}\pi}}\, \mathrm{e}^{\frac{-x^2}{4\cdot\mathrm{D}\cdot 9}}$$

Simple variations on these input files include addition of a constant or simple function on the right to represent current, plus or minus for the augmenting or retarding case. Multiplication of the numerator of the premultiplying factor on the right by 1.8 has been used to represent 80% cloning before settlement of the primary population (red curve) and 0.8 has been used to represent the population after 80% cloning and after settlement (blue curve). This numerator could have been multiplied by a function linear with time or a more complicated function of time to represent mortality.

S.9 References

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SPATIAL AND TEMPORAL APPROACHES IN ANALYZING RECREATIONAL GROUNDFISH DATA FROM SOUTHERN CENTRAL CALIFORNIA AND THEIR APPLICATION TOWARD MARINE PROTECTED AREAS

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ABSTRACT

Many nearshore rockfish species have small home-range sizes and therefore may be affected by heavier localized fishing in near-port areas. For this study we examined long-term trends in rockfish and lingcod landings from the commercial passenger fishing vessel (CPFV) fishery along the south central coast (SCC) of California using data from two sources: California Department of Fish and Game (CDFG) surveys from 1988–98 and California Polytechnic State University (Cal Poly) surveys in 2003–04. The objective was to make comparisons between areas close to port (that receive greater fishing effort) and those far from port (areas receiving less fishing effort). We analyzed parameters for individual species and species assemblage composition to determine if these parameters are effective at detecting changes on a species-specific and a multi-species level for this region and what their applications are towards newly established Marine Protected Areas (MPAs) along the SCC.

A multivariate approach using non-standardized Bray Curtis similarities effectively detected both spatial and temporal changes within and between fish assemblages for areas along the SCC. For individual species, catches of some species yielded larger individuals farther from port, while catch per unit effort (CPUE) for most species did not differ between near-port and distant-port areas over time. Trends were easier to detect for species that exclusively inhabit shallower waters and suggest that these may be better indicator species for examining the effectiveness of MPAs. Results were difficult to interpret for species that occur at mixed depths since some migrate to deeper waters when they mature, whereas others inhabit both shallow and deep depths as adults.

INTRODUCTION

The status of many groundfish stocks and the overall sustainability of California's marine fisheries are in question and are thought to be influenced by fishing pressure and ocean temperatures like many marine populations. Rockfishes (*Sebastes* spp.) are of particular concern to resource managers because they are very long-lived, slow-growing, and late-maturing species that have variable recruitment patterns influenced by a suite of oceanographic conditions (Leaman 1991; Parker et al. 2000; Love et al. 2002). Intensive commercial fishing has reduced population numbers and caused stock collapses for some rockfish species (Ralston 1998). There is also strong evidence that recreational fishing has affected rockfish populations in some regions off California, including the Southern California Bight and areas off Monterey and San Francisco (Karpov et al. 1995; Love et al. 1998a; Mason 1998). In addition, increasing sea-surface temperatures and changing ocean climates have caused such negative population responses as declining catch (Bennett et al. 2004; Jarvis et al. 2004) and declines in recruitment have been associated with a warm regime in a cycle termed the Pacific Decadal Oscillation (PDO) (Stephens et al. 1983, 1984; Love et al. 1998b; Chavez et al. 2003).

As catch rates declined for certain nearshore rockfish species in areas closer to port, recreational fisheries shifted fishing effort toward less fished areas. The commercial passenger fishing vessel (CPFV) fishery began utilizing areas farther from port as early as the 1960s in some regions of central and northern California (Miller and Gotshall 1965). Mason (1995) reported similar trends for the Monterey area, noting an increasing frequency of fishing trips to deeper waters and distant-port areas over a 30-year period (1959–86). This resulted in localized overfishing for several species because of their limited movements, and also led to the truncation of size-age distributions. Reilly et al. (1993) suggested that distance from port and greater depths are factors contributing to a higher catch per unit effort (CPUE) and larger-sized fish for certain rockfish species.

The main objective of this study was to examine individual species trends and changes within fish assemblages between near-port and distant-port areas for the CPFV fishery along the south central coast (SCC) of California. Earlier studies compared trawl and partyboat fisheries (Heimann and Miller 1960), sportfish catch and effort from 1957–61 (Miller and Gotshall 1965), and life-history characteristics for blue rockfish (*Sebastes mystinus*) and lingcod (*Opiodon longatus*) (Miller et al. 1967; Miller and Geibel 1973). In addition, Karpov et al. (1995) made historical comparisons between the Miller and

Gotshall (1965) sportfish data and the Marine Recreational Fishery Statistical Survey (MRFSS) data from 1980–86, and Stephens et al. (2006) conducted an analysis of the groundfish fishery. Here we use data from a CPFV California Department of Fish and Game (CDFG) survey (1988–98) and a California Polytechnic State University survey (2003–04) to examine whether it may be possible to use individual species trends and a multi-species approach as a means to determine if greater fishing effort at near-port areas has had an impact on these species.

Additionally, we wanted to see how these approaches might be used as a means to track the effectiveness of the newly established "no-take" Marine Protected Areas along the SCC. Since different rockfish species occupy different types of habitats and various depth ranges, species are unlikely to benefit equally. Thus, another objective of this study was to use the comparison of near-port and distant-port areas as a means to compare areas with greater fishing effort to those with less fishing effort to see which species are most likely to benefit from the MPAs and thus, to track their effectiveness over time.

MATERIALS AND METHODS

Study Area

The Morro Bay South-Central Management Area includes all of the SCC, encompasses the region between Lopez Point (36°01'N, 121°34'W) and Point Conception (34°27'N, 120°28'W), and includes two major port areas, Morro Bay and Avila (Port San Luis). Lopez Point is the farthest distance traveled north by CPFVs leaving from Morro Bay, and Purisima Point (34°45'N, 120°38'W) is the farthest point south for vessels leaving Port San Luis. CPFVs from Morro Bay generally fish in the northern area from Point Buchon to Lopez Point, while those from Port San Luis mostly fish in the southern area from Point Buchon to Purisima Point (fig. 1).

The northern and southern regions were further subdivided into near-port and distant-port areas. The areas in the northern region include "Morro near," which includes near-port areas between Point Buchon and south of San Simeon, and "San Simeon north," which includes distant-port areas from San Simeon northward. The southern region areas include "Avila near," which includes near-port areas between Port San Luis and Point Buchon, and "Point Sal/Purisima," which includes distant-port areas fished from Port San Luis.

The SCC is an ideal region in which to use comparisons of species aggregations in near-port and distant areas to examine whether heavier localized fishing in near-port areas had noticeable effects on local fish populations. As noted earlier, the proportion of trips to areas distant from port increased greatly for the Monterey region over a 30-year period (Mason 1995), and in addition, high percentages of trips to distant locations (>50%) have been reported for the Bodega Bay and San Francisco regions (Wilson et al. 1996). While these regions have experienced increased fishing effort in distant locations, the percentage of trips to distant-port areas in the SCC has changed very little (<15%) over time (Reilly et al. 1993, Wilson et al. 1996). During the 2003–04 seasons, near-port fishing trips occurred five to seven days a week with sometimes several boats fishing these areas per day, while distant-port or "long-range" trips occurred once or twice a week with only one boat fishing the area.

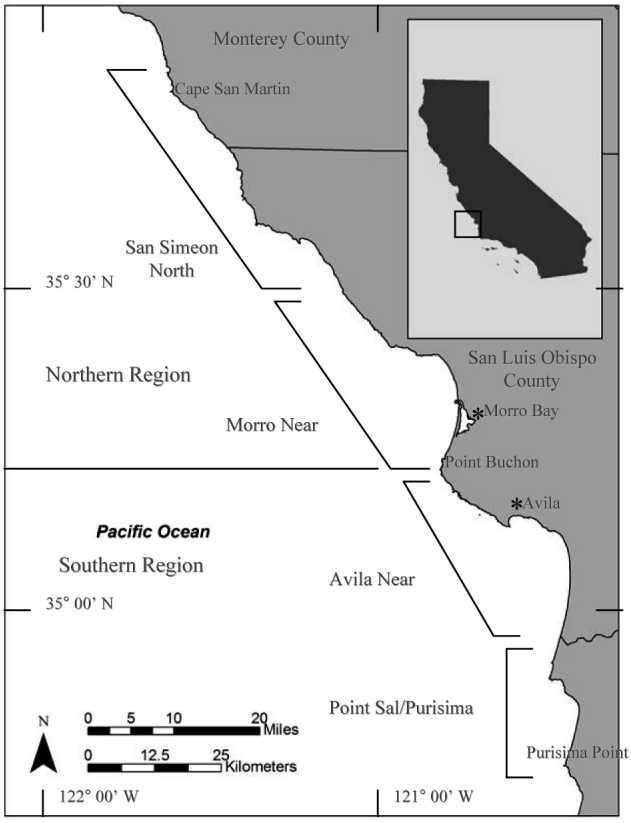

Figure 1. The Morro Bay CPFV region showing near-port and distant-port areas. Port areas indicated with an *.

Sampling Procedure

Data collected from CPFVs for the sportfishing groundfish fishery in 2003–04 were obtained from a collaborative research effort between CPFV vessels out of Port San Luis (Patriot Sportfishing) and Morro Bay (Virg's Sportfishing) and scientists from the Center for Coastal Marine Sciences at California Polytechnic State University (Cal Poly) in 2003–04. Two student observers accompanied CPFV vessels on trips that were targeting rockfish and lingcod and sampled the total catch of a subset of the total fishermen aboard the vessel, usually between six to 14 individuals. Observers recorded the

number of observed fishers, total fishing time, GPS location, and water depth at each fishing locality. Within the subset of observed fishers the observers recorded the species caught, measured fish size in fork length to the nearest 0.5 cm, and recorded the disposition of each individual fish ("K-" for kept fish, "RA-" for fish released alive, and "RD-" for fish released dead).

Additionally, CPFV data taken by CDFG samplers from 1988–98 for the SCC were made available in Microsoft Access format. These data are partially available as unpublished administrative reports (Reilly et al. 1993, 1998; Wilson et al. 1996; Wilson-Vandenberg et al. 1995, 1996). For a more detailed description of the methods used by the CDFG survey, see Reilly et al. (1993). The Cal Poly and CDFG data sets were comparable as both protocols followed similar methodologies and contained area and depth specific information on where fish were caught. Prior to these two data sets, information was not available on an area-specific basis in central California, but rather summed up on a regional basis or by county district (Miller and Gotshall 1965; Karpov et al. 1995). Area-specific and depth-specific information, along with measurements for released fish, are available for certain areas in the Southern California Bight, including the Channel Islands, dating back to 1975 (Love et al.1985).

The Cal Poly protocol was similar to that in the Channel Islands study in that fish lengths were recorded at each fishing location throughout the day and released fish were also measured. The CDFG survey differed in that fish lengths were recorded at the end of the day, and only kept fish were measured. For individual species, CPUE can be compared between the CDFG and Cal Poly surveys since area- and depth-specific information were available. But fish lengths were only used from the Cal Poly survey because it was difficult to obtain accurate area and depth-specific data for fish lengths in the CDFG study and we did not want to introduce a size bias by including measurements of retained or kept fish.

Statistical Analysis

We used a multivariate approach with non-standardized Bray Curtis similarity indices to determine the similarity between fish assemblages from near-port and fish assemblages from distant-port areas along the SCC. We tested whether species catch rates were similar between both near-port areas since they receive similar fishing effort. The same test was applied to distant-port areas. Similarity of species catch rates from these areas was analyzed using the ANOSIM analysis from the Primer 5 statistics package (PREMEIR Biosoft International). A significance level greater than 5.0% for comparisons of two or more areas indicates that the fish assemblages are not significantly different between these areas, whereas values <5% indicate that there are differences in species catch rates between same-type areas, suggesting that fish assemblages from those areas are not similar.

Species catch rates were determined through CPUE. CPUE for each species was calculated by dividing the total catch by the number of angler hours, where angler hours = (average number of anglers * the number of minutes) / 60. Yearly CPUE values for the most abundant species were used to compare species assemblage compositions between areas. Species were selected based on abundance throughout the entire study and only species that made up ≥1% of the total recreational catch in waters ≤55 m (30 fm) from 1988–2004 were used in the analysis. A depth of 55 m (30 fm) was used for both the CDFG and Cal Poly data sets to reflect regulation changes that occurred during 2003–04. Sampling of distant-port areas at Point Sal/Purisima did not begin until 1989, and sampling of distant-port areas from San Simeon north began in 1991. Also, there were years when not enough data were available for near-port areas mainly due to a concentration on deeper-water fishing. Data from such years were excluded from the analysis.

Multi-Dimensional Scaling (MDS) plots with subsequent Cluster Analysis (CA) using 70% confidence level limits were used to assess similarity in species assemblage composition between areas. A tighter cluster between years for a particular area indicates a high degree of similarity among years, whereas a more loosely associated cluster indicates a variable catch composition between years. Similarly, a tighter cluster between comparisons of two areas indicates that fish assemblages are similar between these areas, while separate and more distinct clusters indicate that the assemblages are different for those areas. Dotted circles were drawn around each of the major areas where applicable to give an idea of how similar or different assemblages from these areas were to each other.

Annual mean sea-surface temperature (SST) anomalies were used as proxies for oceanographic events to explain shifts in assemblage composition. The annual mean SSTs were obtained by calculating the daily mean of the measurements made by the Cape San Martin (#46028) and Santa Maria (#46011) NOAA buoys and then averaging those daily means over each year (www.ndbc.noaa.gov).

A Kruskal-Wallis test was used for each species to determine if size-class distributions were different between near-port and distant-port areas. The more powerful parametric tests, a one-way ANOVA or a *t*-test, could not be used because the assumptions of normality and equal variance were not met.

The general linear ANOVA model was used to analyze CPUE between near and distant-port areas for each species. To fit normality assumptions, CPUE values were square-root transformed. Since regulations regarding the

TABLE 1
Species abundance listed by CPUE per year for near-port and distant-port areas for the top 12 species along the south central Coast.

A. San Simeon North

Species	1991	1992	1993	1994	1995	1996	1997	1998	2003	2004	Mean
Blue rockfish	1.84	2.48	2.17	1.57	0.94	1.89	3.28	3.05	2.46	3.21	2.29
Gopher rockfish	0.69	0.94	0.49	0.57	1.07	1.25	0.87	1.22	1.27	0.48	0.89
Olive rockfish	0.87	0.48	0.39	0.30	0.54	0.26	0.17	0.35	0.32	0.42	0.41
Lingcod	0.12	0.14	0.13	0.14	0.21	0.29	0.32	0.57	0.61	0.52	0.31
Vermilion rockfish	0.14	0.12	0.16	0.24	0.19	0.13	0.24	0.24	0.51	0.62	0.26
Yellowtail rockfish	0.19	0.10	0.21	0.41	0.14	0.18	0.11	0.11	0.05	0.19	0.17
Copper rockfish	0.10	0.10	0.09	0.06	0.10	0.11	0.07	0.02	0.09	0.26	0.10
Starry rockfish	0.24	0.12	0.05	0.10	0.01	0.13	0.08	0.00	0.07	0.10	0.09
Rosy rockfish	0.09	0.08	0.07	0.09	0.03	0.09	0.10	0.00	0.11	0.09	0.08
Canary rockfish	0.07	0.03	0.01	0.08	0.08	0.01	0.03	0.02	0.04	0.05	0.04
Black rockfish	0.16	0.00	0.02	0.16	0.03	0.02	0.01	0.00	0.00	0.02	0.04
Brown rockfish	0.01	0.05	0.03	0.01	0.01	0.05	0.01	0.00	0.14	0.07	0.04

B. Morro Near

Species	1988	1989	1991	1992	1993	1994	1995	1996	1997	1998	2003	2004	Mean
Blue rockfish	0.29	0.40	0.81	1.58	2.69	2.20	1.09	1.40	3.60	5.45	1.51	2.78	1.98
Gopher rockfish	0.40	0.38	0.32	0.56	0.40	0.59	0.56	0.79	0.46	0.86	1.16	0.91	0.62
Yellowtail rockfish	0.29	0.47	0.10	0.46	0.78	1.03	0.39	0.26	0.22	0.11	0.10	0.16	0.36
Vermilion rockfish	0.26	0.28	0.03	0.21	0.21	0.16	0.11	0.15	0.19	0.24	0.26	0.55	0.22
Olive rockfish	0.02	0.00	0.57	0.32	0.16	0.09	0.15	0.29	0.19	0.47	0.09	0.11	0.21
Lingcod	0.06	0.03	0.10	0.17	0.07	0.10	0.15	0.25	0.31	0.26	0.38	0.43	0.19
Rosy rockfish	0.13	0.19	0.08	0.19	0.32	0.38	0.16	0.21	0.07	0.05	0.08	0.10	0.16
Canary rockfish	0.14	0.09	0.04	0.18	0.10	0.06	0.11	0.15	0.04	0.06	0.03	0.11	0.09
Brown rockfish	0.00	0.00	0.33	0.01	0.01	0.04	0.08	0.06	0.00	0.05	0.27	0.10	0.08
Black rockfish	0.00	0.00	0.41	0.01	0.01	0.00	0.03	0.07	0.11	0.03	0.08	0.01	0.06
Copper rockfish	0.09	0.02	0.06	0.10	0.09	0.06	0.04	0.06	0.04	0.04	0.03	0.06	0.06
Starry rockfish	0.09	0.02	0.06	0.10	0.09	0.06	0.04	0.06	0.04	0.04	0.03	0.06	0.06

C. Avila Near

Species	1988	1989	1991	1992	1993	1994	1995	1996	1997	1998	2003	2004	Mean
Blue rockfish	0.52	0.18	0.72	1.65	2.04	0.77	1.20	1.55	2.33	2.16	1.91	3.22	1.52
Yellowtail rockfish	0.35	0.92	0.22	0.88	0.67	0.79	0.40	0.31	0.30	0.31	0.14	0.23	0.46
Gopher rockfish	0.11	0.21	0.11	0.26	0.63	0.31	0.24	0.33	0.29	0.30	0.89	0.69	0.36
Vermilion rockfish	0.17	0.41	0.05	0.14	0.24	0.28	0.08	0.10	0.21	0.17	0.49	0.68	0.25
Rosy rockfish	0.18	0.27	0.16	0.14	0.31	0.32	0.12	0.16	0.04	0.13	0.08	0.18	0.17
Lingcod	0.09	0.38	0.04	0.16	0.14	0.14	0.17	0.28	0.30	0.11	0.51	0.36	0.22
Brown rockfish	0.00	0.03	0.00	0.26	0.24	0.10	0.12	0.04	0.19	0.31	0.61	0.20	0.18
Olive rockfish	0.00	0.00	0.08	0.26	0.22	0.05	0.10	0.06	0.10	0.07	0.13	0.09	0.10
Copper rockfish	0.11	0.20	0.00	0.09	0.06	0.19	0.07	0.10	0.07	0.12	0.04	0.08	0.09
Starry rockfish	0.11	0.20	0.00	0.09	0.06	0.19	0.07	0.10	0.07	0.12	0.04	0.08	0.09
Black rockfish	0.00	0.00	0.05	0.00	0.10	0.05	0.00	0.00	0.04	0.01	0.06	0.01	0.03
Canary rockfish	0.07	0.14	0.00	0.05	0.05	0.05	0.06	0.09	0.06	0.03	0.02	0.04	0.06

D. Point Sal/Purisima

Species	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	2003	2004	Mean
Brown rockfish	1.94	1.19	1.38	1.23	0.39	1.20	2.13	1.09	0.52	1.77	1.52	1.63	1.33
Blue rockfish	0.90	0.13	0.81	1.03	0.13	0.28	0.76	0.29	1.47	2.78	1.54	1.35	0.96
Gopher rockfish	1.32	0.83	0.51	0.50	0.36	0.61	0.80	0.75	0.71	0.87	0.50	0.84	0.72
Yellowtail rockfish	1.56	0.05	0.03	0.11	0.06	0.68	0.77	0.48	0.18	0.29	0.10	0.16	0.37
Lingcod	0.31	0.23	0.45	0.28	0.05	0.07	0.43	0.27	0.38	0.28	0.41	0.60	0.31
Olive rockfish	0.21	0.50	0.48	0.14	0.16	0.13	0.26	0.22	0.62	0.00	0.34	0.19	0.27
Vermilion rockfish	0.24	0.13	0.10	0.12	0.10	0.16	0.19	0.11	0.22	0.30	0.37	0.63	0.22
Black rockfish	0.00	0.67	0.94	0.30	0.17	0.12	0.04	0.05	0.09	0.03	0.10	0.02	0.21
Copper rockfish	0.21	0.03	0.08	0.05	0.18	0.05	0.14	0.09	0.11	0.08	0.02	0.07	0.09
Canary rockfish	0.14	0.08	0.02	0.00	0.06	0.24	0.20	0.14	0.05	0.04	0.04	0.02	0.09
Rosy rockfish	0.00	0.00	0.00	0.06	0.09	0.01	0.04	0.09	0.08	0.10	0.04	0.05	0.05
Starry rockfish	0.00	0.00	0.00	0.01	0.01	0.00	0.01	0.01	0.00	0.01	0.00	0.00	0.00

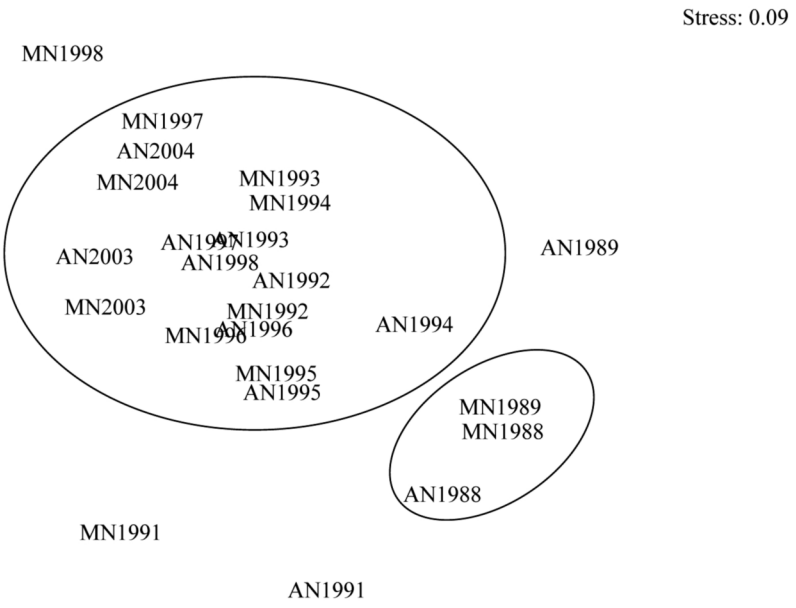

Figure 2. Bray-Curtis Multi-Dimensional Scaling plot for comparisons in species catch composition between the two near-port areas (MN = Morro Near, AN = Avila Near).

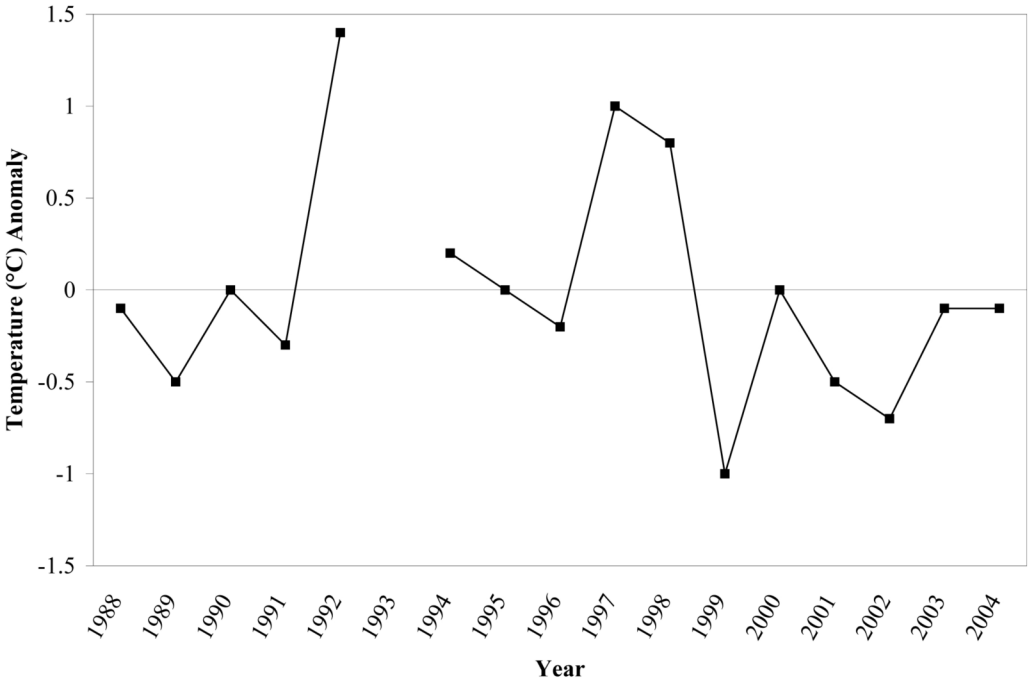

Figure 3. Annual sea surface temperature anomalies derived from daily readings taken at NOAA buoys 46028 at Cape San Martin, Monterey County, California, and 46011 at Santa Maria, Santa Barbara County, California. No data were recorded for either site in 1993.

number of allowable hooks and bag limit sizes were different between the CDFG and Cal Poly surveys, CPUEs were analyzed separately for each survey. Daily CPUE values were used rather than single yearly values because they account for greater variability. This model accounted for monthly, yearly, and area variations between near-port and distant-port areas for each species.

RESULTS

Spatial and Temporal Patterns for Fish Assemblages

Spatial and temporal patterns of fish assemblages for near- and distant-port areas are listed in Table 1. An analysis of species assemblage composition for the two

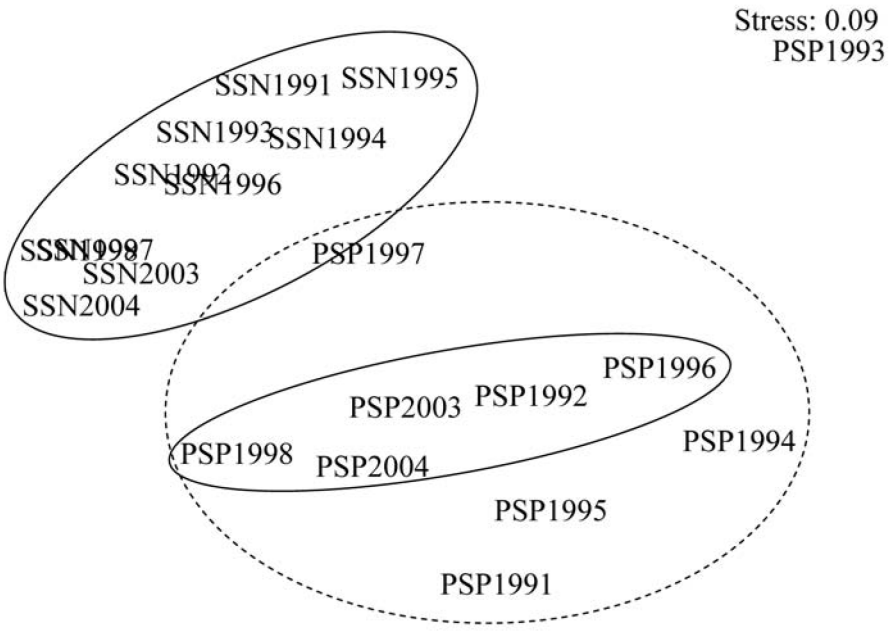

Figure 4. Bray-Curtis Multi-Dimensional Scaling plot for comparisons in species catch composition between the two distant-port areas (SSN = San Simeon north, PSP = Point Sal/Purisima).

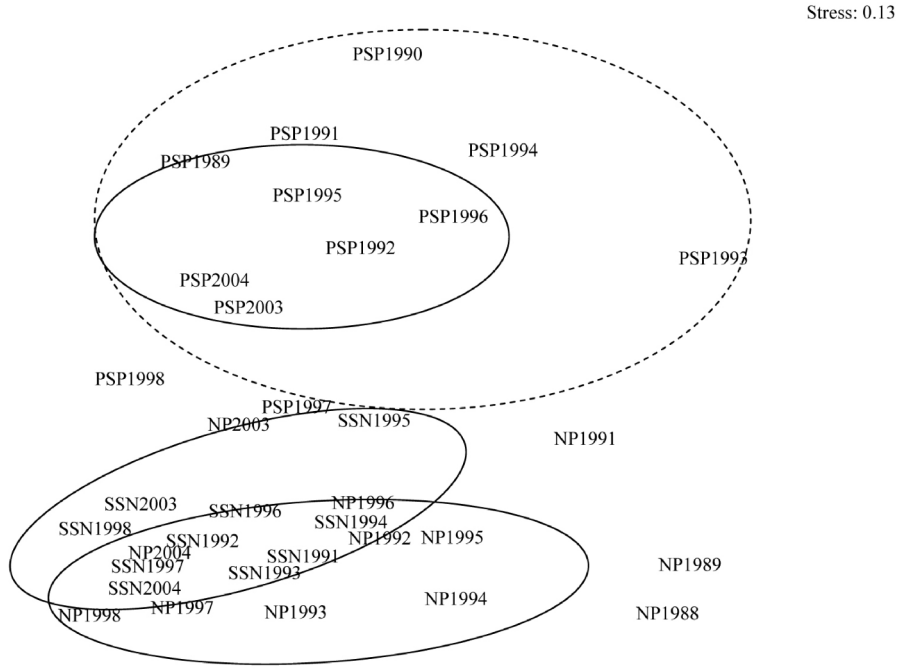

Figure 5. Bray-Curtis Multi-Dimensional Scaling plot for comparisons in species catch composition between near-port and distant-port areas (NP = near-port areas, SSN = San Simeon north, and PSP = Point Sal/Purisima).

near-port areas indicates that there was no significant difference between these areas (Significance level = 28%, $R = 0.019$). The Multi-Dimensional Scaling (MDS) plot for these areas had many close comparisons (fig. 2). There was a smaller separate cluster for some earlier years compared to a larger cluster for later years. Outlying years were 1991 for both sites, 1989 for the Avila near area, and 1998 for the Morro near area. Annual SSTs for the earlier years correspond to cooler years, while 1998 was a warmer El Niño year (fig. 3).

There was a significant difference in catch composition between the distant-port areas (Significance level = 0.1%, $R = 0.679$). The MDS plot for these areas shows a clear separation between the two areas (fig. 4) with a

TABLE 2

Median length and standard deviation between near-port areas and distant-port areas at San Simeon north for the top 11 species. Differences among distributions were tested on the median length using a Kruskal-Wallis test and were considered significant at $p \leq 0.05$. Significant differences for individual species are indicated by *.

	Near-port			Distant-port			
Species	Median Length (cm)	SD	*n*	Median Length (cm)	SD	*n*	*P*
Blue rockfish	27.00	4.56	9357	29.00	4.34	1741	<0.001*
Brown rockfish	34.50	3.88	1071	36.00	3.34	61	<0.001*
Canary rockfish	30.25	3.95	215	30.00	2.79	30	0.404
Copper rockfish	33.00	5.71	218	38.00	5.50	123	<0.001*
Gopher rockfish	26.50	2.32	3508	26.75	2.36	480	0.039*
Olive rockfish	30.50	6.78	417	37.50	6.51	239	<0.001*
Rosy rockfish	20.50	2.34	440	20.00	2.59	59	0.779
Starry rockfish	31.00	3.25	202	32.00	5.03	54	0.049*
Vermilion rockfish	32.00	6.65	2039	41.00	6.23	359	<0.001*
Yellowtail rockfish	20.00	5.82	587	27.50	4.20	78	<0.001*
Lingcod	54.00	8.31	1519	57.00	9.47	324	<0.001*

tighter cluster between years for the San Simeon north area. As indicated by a more loosely associated cluster and many outlying years, species composition of the catch in the Point Sal/Purisima area was highly variable among years.

Since the near-port areas were so similar in assemblage composition and fishing effort, we combined the data from the Avila and Morro near-port areas to compare with data from each of the distant-port areas. The combined catch composition of the near-port areas was only slightly different from that of San Simeon north (Significance level = 4.3%, $R = 0.153$), while catch from near-port areas and Point Sal/Purisima were very different (Significance level = 0.1%, $R = 0.544$). The species composition for San Simeon north was tightly clustered among years, while near-port areas showed a higher degree of inter-annual variation in species composition. Although there was a fair amount of overlap between these areas, the most anomalous years for near-port areas occurred during 1988–91, which were larger than the outliers for San Simeon north (fig. 5). Conversely, the catch composition from the Point Sal/Purisima area was clearly distinct from other areas and exhibited a loosely associated cluster with many outlying years.

The assemblage for the Point Sal/Purisima area was markedly different from the other assemblages in two major ways. First, fish assemblages at San Simeon north and near-port areas changed less over time than the assemblage at Point Sal/Purisima, as the MDS plots indicate (figs. 2, 4, and 5). Second, brown rockfish (*Sebastes auriculatus*) was the predominant species in catches from this region, whereas blue rockfish (*Sebastes mystinus*) was the most abundant species in catches from all other areas (tab. 1). Brown rockfish CPUE was consistently high throughout the study at the Point Sal/Purisima area and this species was the most abundant in nearly every year sampled, while it was typically among the least abundant in the other two areas.

Length Comparisons Between Near- and Distant-port Areas (2003–04)

Since fishing effort and assemblage composition were similar between near-port areas (fig. 2), data on fish lengths were combined for these areas and compared separately to distant areas. Differences in size-class distributions for 10 rockfish species and lingcod were compared between near-port areas and San Simeon north (tab. 2) and Point Sal/Purisima (tab. 3) using the Kruskal-Wallis method. Overall, three patterns were apparent in this fishery regarding species size as a function of distance fished from port: (1) some species were always larger for distant-port areas; (2) some species were larger in the north than south; and (3) some species showed little or no difference in length between near- and distant-port areas. Olive (*Sebastes serranoides*) and vermilion (*S. miniatus*) rockfish were exceptions to these trends.

Brown, copper (*S. caurinus*), and starry (*S. constellatus*) rockfishes and lingcod fit the first category in which fish sizes were always larger for distant-port areas with less fishing effort than near-port areas. Length differences were highly pronounced for copper rockfish, whose median length was 5 cm larger for San Simeon north and 7 cm larger for the Point Sal/Purisima area. Lingcod measurements were 3 cm larger for San Simeon north and 6 cm larger for the Point Sal/Purisima area. Additionally, brown rockfish were larger for both distant-port areas compared to near-port areas. Although there was only a 1 cm difference between the starry rockfish measurements from near- and distant-port areas in San Simeon north, the species was slightly larger in San Simeon north than the combined near-port areas; the results were significant ($p = 0.049$, tab. 2).

Olive and vermilion rockfish were significantly larger in distant-port areas compared to near-port areas in the San Simeon north area with median lengths of 7 and 9 cm greater, respectively. Although both of these species were much larger in size in the San Simeon north area

TABLE 3

Median length and standard deviation between near-port areas and distant-port areas at Point Sal/Purisima north for the top 11 species. Differences among distributions were tested on the median length using a Kruskal-Wallis test and were considered significant at $p \leq 0.05$. Significant differences for individual species are indicated by *.

	Near-port			Distant-port			
Species	Median Length (cm)	SD	*n*	Median Length (cm)	SD	*n*	*P*
Blue rockfish	27.00	4.56	9347	25.00	4.68	831	<0.001*
Brown rockfish	34.50	3.88	1071	37.50	4.66	979	<0.001*
Canary rockfish	30.25	3.95	215	29.00	3.51	15	0.545
Copper rockfish	33.00	5.71	218	40.00	7.08	30	<0.001*
Gopher rockfish	26.50	2.32	3508	26.00	1.98	443	0.031*
Olive rockfish	30.50	6.78	417	32.25	7.88	150	0.093
Rosy rockfish	20.50	2.34	440	21.50	2.13	25	0.034*
Starry rockfish	31.00	3.25	202	—	—	—	—
Vermilion rockfish	32.00	6.65	2039	31.50	8.11	331	0.338
Yellowtail rockfish	20.00	5.82	587	18.50	4.64	75	<0.001*
Lingcod	54.00	8.31	1519	60.00	9.48	295	<0.001*

TABLE 4

Comparisons of CPUE between near- and distant-port areas at San Simeon north for the top 11 species. † indicates significant differences in CPUE between near and distant areas for 1988–98, * indicates those of 2003–04, and *† indicates those for both periods; − indicates cases where the assumptions of the general linear ANOVA were not met.

	1988–1998			2003–2004		
Species	Month	Year	Area	Month	Year	Area
Blue rockfish	0.457	<0.001	0.679	<0.001	<0.001	0.872
Brown rockfish	—	—	—	—	—	—
Canary rockfish	0.009	0.183	0.003†	0.001	0.753	0.882
Copper rockfish	0.364	0.182	0.619	0.004	0.599	<0.001*
Gopher rockfish	0.682	0.061	<0.001†	0.004	0.001	0.057
Olive rockfish	0.062	<0.001	<0.001*†	0.003	0.421	<0.001*†
Rosy rockfish	0.152	0.055	<0.001†	0.001	0.644	0.409
Starry rockfish	0.737	0.304	0.426	0.529	0.057	0.025*
Vermilion rockfish	0.125	0.016	0.235	<0.001	0.668	0.409
Yellowtail rockfish	0.097	<0.001	<0.001†	0.001	0.533	0.654
Lingcod	0.166	0.011	0.211	0.017	0.009	0.045*

there were no significant differences in size-class distributions for these species between near-port areas and the Point Sal/Purisima area (tab. 3). Blue and yellowtail (*S. flavidus*) rockfish were larger sized for San Simeon north compared to the combined near-port areas, but the patterns were different for the Point Sal/Purisima area.

Blue and yellowtail rockfish fit the second category where fish lengths followed a north to south gradient with smaller fish found farther south. This pattern was more pronounced for yellowtail rockfish than blue rockfish. Median lengths for yellowtail rockfish from north to south were 27.5 (San Simeon north), 20 (near-port), and 18.5 cm (Point Sal/Purisima), while they were 29, 27, and 25 cm for blue rockfish (tabs. 2 and 3).

The remaining species fit the third category where little or no differences in length were observed between near- and distant-port areas. There were no differences in canary rockfish (*S. pinniger*) size distributions between near- and distant-port areas (Kruskal-Wallis test, near-port vs. San Simeon north, $p = 0.404$, tab. 2; near-port vs. Point Sal/Purisima, $p = 0.545$, tab. 3); however, significant differences were detected for the Point Sal/Purisima area for rosy rockfish (*S. rosaceus*) and for both distant-port areas for gopher rockfish (*S. carnatus*, tabs. 2, 3). While differences in length between near- and distant-port areas for both of these species are statistically significant (tabs. 2, 3), a large sample size and the small species catch size range may have masked an apparent trend.

Size-class distributions were significantly different for nine of the 11 species when comparing those from near-port areas to those from San Simeon north (tab. 2). In each case, examined lengths from distant-port areas. Conversely, differences in size-class distributions were detected for seven of 11 species with three having larger sizes in near-port areas when compared to the Point Sal/Purisima area (tab. 3). This may suggest a north-south cline for these species.

CPUE Between Near- and Distant-port Areas (1988–2004)

During the CDFG surveys, CPUE for the different species exhibited one of four major patterns: (1) CPUE

TABLE 5

Comparisons of CPUE between near and distant areas at Point Sal/Purisima north for the top 11 species. † indicates significant differences in CPUE between near and distant areas for 1988–98, * indicates those of 2003–04, and *† indicates those for both periods; – indicates cases where the assumptions of the general linear ANOVA were not met.

	1988–1998			2003–2004		
Species	Month	Year	Area	Month	Year	Area
Blue rockfish	0.298	<0.001	0.002*†	<0.001	0.002	<0.001*†
Brown rockfish	—	—	—	—	—	—
Canary rockfish	0.080	0.020	0.545	<0.001	0.581	0.348
Copper rockfish	0.174	0.347	0.003†	0.001	0.170	0.815
Gopher rockfish	0.658	0.116	0.009†	<0.001	0.234	0.134
Olive rockfish	0.036	<0.001	0.009*†	0.018	0.115	0.004*†
Rosy rockfish	0.175	0.128	0.041†	0.001	0.721	0.131
Starry rockfish	0.673	0.117	0.003†	—	—	—
Vermilion rockfish	0.134	0.013	0.196	<0.001	0.734	0.186
Yellowtail rockfish	0.790	0.002	0.495	<0.001	0.480	0.361
Lingcod	0.435	0.064	0.113	0.054	0.114	0.078

did not differ between near- and distant-port areas during 1988–98 but differed significantly during 2003–04; (2) CPUE differed between near- and distant-port areas during 1988–98 but not during 2003–04; (3) CPUE did not differ at all between near- and distant-port areas during surveys in either period; and (4) CPUE differed between near- and distant-port areas during surveys in both periods.

CPUE values for lingcod, starry rockfish, and copper rockfish were not significantly different between near- and distant-port areas from 1988–98, but were during 2003–04 (tabs. 4 and 5). CPUE in 2003–04 was higher for distant-port areas for starry rockfish (fig. 6H). This also was true for lingcod and copper rockfish, but only when compared with San Simeon north (figs. 6D and J).

Catch rates for gopher and rosy rockfish were significantly different between near- and distant-port areas from 1988–98 but not during 2003–04 (tabs. 4 and 5). However, the CPUE for gopher rockfish was generally lower for near-port areas from 1988–98, while it was generally higher for rosy rockfish (figs. 6E and G). CPUEs for canary and yellowtail rockfish were also higher for near-port areas during 1988–98, but only when compared to San Simeon north (figs. 6C and J). CPUE for these two species did not differ significantly between near-port areas and the Point Sal/Purisima area. CPUE for copper was higher in distant-port areas during 1988–98, but only for the Point Sal/Purisima area (fig. 6D).

There were a few species for which CPUE was the same between near- and distant-port areas in both surveys. CPUE for vermilion rockfish did not differ between any of the areas; while for blue rockfish no differences in CPUE were detected between near-port areas and San Simeon north (tab. 4), nor for canary and yellowtail rockfish between near-port areas and Point Sal/Purisima (tab. 5).

CPUE patterns for olive and brown rockfish differed from the above mentioned trends. For olive rockfish, CPUE was always highest for distant-port areas during both surveys (tabs. 4, 5). The assumptions of the general linear ANOVA model were not met for brown rockfish because it was scarce throughout most of the study area. However, the plot of CPUE between near- and distant-port areas (fig. 6B) indicates that this species is only abundant in distant-port areas at the Point Sal/Purisima area, with catch rates several times higher in magnitude for this region compared to other areas.

DISCUSSION

Our multivariate analysis demonstrated clear spatial and temporal patterns in fish assemblages over different areas in the SCC by applying a multivariate approach using Bray-Curtis similarity indices. Fish assemblages from the two near-port areas were similar, while distant-port areas were markedly different both from each other and from near-port areas. The tight clustering between years for the San Simeon north area in the MDS plot suggests that this area has remained fairly stable over time (fig. 4). While changes have occurred in near-port areas, the tight clustering between years in the MDS plot for these sites indicates that these areas are similar (fig. 2). Assemblage composition in the near-port areas was not as stable as at San Simeon north, and had two separate clusters while San Simeon north had one tight cluster (figs. 2 and 4). Although greater fishing effort in near-port areas might easily explain some of these differences, these areas may also be influenced by environmental variability, with notable changes occurring during extended periods of cooler water (figs. 2 and 3). A loosely associated cluster with many outlying years and a clear separation in catch composition compared to other areas indicates that the Point Sal/Purisima area assemblage is highly variable and different than anywhere else along the SCC.

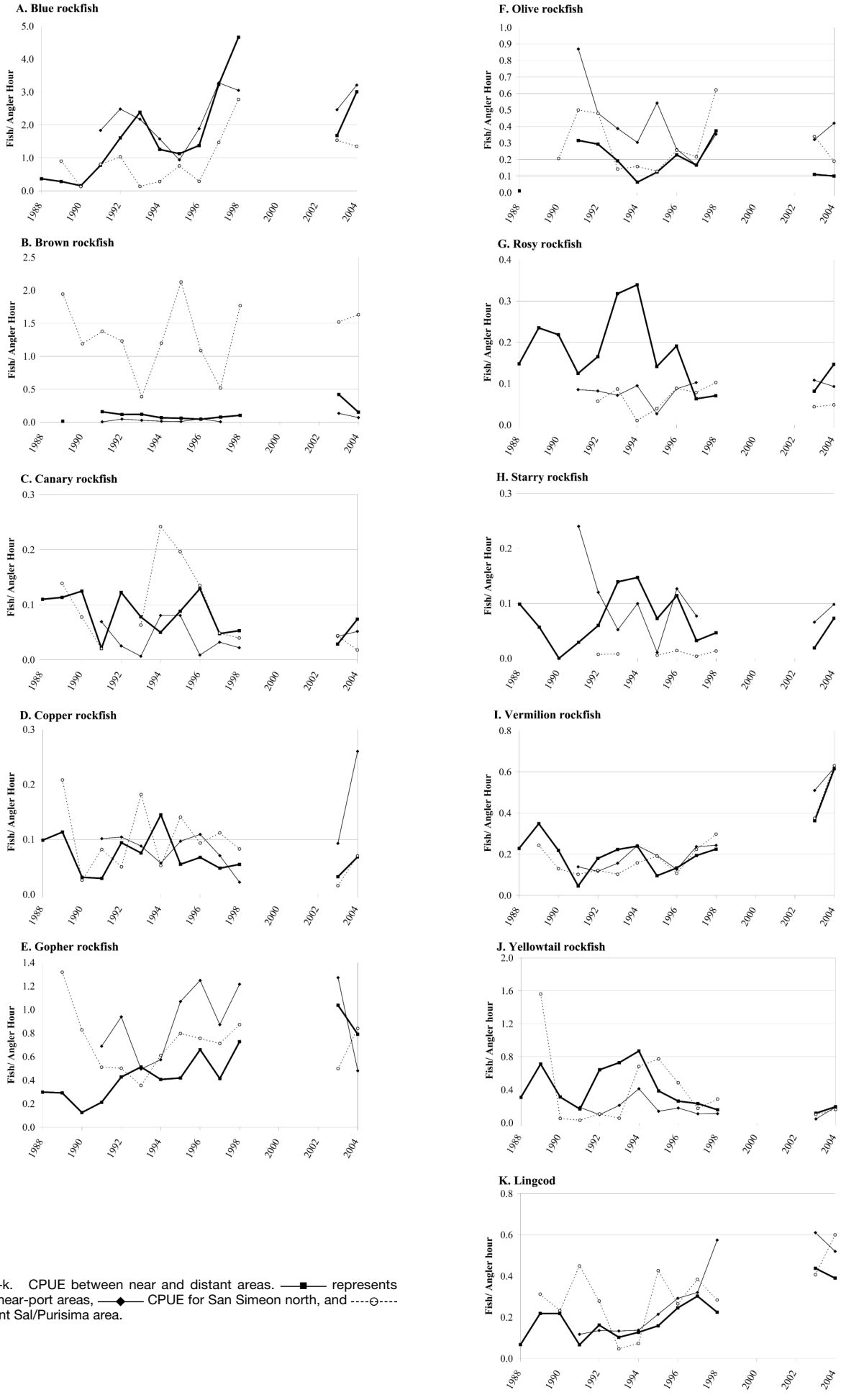

Figure 6a–k. CPUE between near and distant areas. —■— represents CPUE for near-port areas, —◆— CPUE for San Simeon north, and ----⊖---- for the Point Sal/Purisima area.

The fish assemblage in the Point Sal/Purisima area was the least stable of the four areas over time, despite lower fishing effort. Some of this variation may have been due to fluctuating sea surface temperatures during El Niño years and from the close proximity of this area to Point Conception, rather than to fishing. Also, the smaller number of fishing days sampled could have produced sampling error (R. Larson, pers. comm.). This area, which is closest to Point Conception, is at a transitional region between warmer temperate waters of the Southern California Bight south of Point Conception and cooler temperate waters (Oregonian) to the north.

Abundant brown rockfish and an overall lower abundance of blue rockfish in the Point Sal/Purisima area may reflect habitat differences. This area consists primarily of low-relief rocky outcrops, while high-relief rocky structures are typical of most of the rest of headland areas in the SCC. Brown rockfish typically utilize low-relief habitats (Love 1996), while species such as blue rockfish typically utilize high-relief structures (Love et al. 2002), which may explain why fewer blue rockfish were caught in this area. Habitat differences may also have influenced the patterns observed for temporal stability of the fish assemblage at the Point Sal/Purisima area. Research by Malatesta and Auster (1999) suggests that where the continental shelf consists of low-relief structures, it is not a homogeneous environment but rather consists of an array of habitats that can change depending on the intensity of storms, which can cover or expose rocky outcrops with sand.

The response to increased fishing effort in near-port areas differed among species, and indicates that not all species respond similarly to fishing effort along the SCC. Several factors may explain this. One is that several species migrate from shallower to deeper waters during their life cycle, and hence differences in length-frequency distributions between near-port and distant-port areas may not be found. Canary and yellowtail rockfish fit this profile; juveniles occur in shallow waters while adults typically prefer deeper depths (Love et al. 1990; Mason 1998). There were no size differences for canary rockfish between near- and distant-port areas, whereas yellowtail rockfish were generally larger sized to the north. Both canary and yellowtail rockfish have a more northerly distribution and are near the southern extent of their range along the SCC (Miller and Lea 1972; Eschmeyer et al. 1983). Few canary rockfish adults, if any, were present in our study, suggesting that while a higher proportion of adults occur farther north, younger fish may recruit to the area via southerly transport along the California Current. The fact that fewer adult yellowtail rockfish were present in the southern portion for this region supports the findings of Reilly et al. (1993) that recruitment to the fishery along this region may not depend on local adult populations but rather on adult populations to the north.

Some species of rockfish do not easily fit into specific depth ranges or categories, and thus trends between near-port and distant-port areas may not always apply under these circumstances. Copper and vermilion rockfishes are classified as all-depth species where adults are common in both shallow and deeper depths (Karpov et al. 1995). Similarly, rosy and starry rockfishes also have adults that occur in both shallow and deeper depths (Love et al. 1990; Eschmeyer et al. 1983), although adults are more common in deeper waters (Love et al. 1990). CPUE in this study was not consistent between near- and distant-port areas or between the CDFG and Cal Poly surveys for these species. This suggests that any differences detected in CPUE may not be a good indicator of stress from increased fishing effort in near-port areas. CPUE was also found not to be a reliable indicator of abundance for pelagic species of tuna in the Pacific Ocean because it does not account for shifts in fishing effort towards other species and ignores the impact of environmentally-induced recruitment variation (Hampton et al. 2005).

Although it may be possible that CPUE does scale with abundance, it appears that fishing has not had a detectable impact on fish densities. However, differences in size-class distributions may serve as better indicators of stress from increased fishing effort for near-port areas than does CPUE, particularly for species whose adults inhabit both shallow and deep waters. Fish size was significantly larger in distant-port areas when there was less fishing effort on shallow-water copper and vermilion rockfish (tabs. 4 and 5). Although adults for these two species occupy both shallow and deep water, it is surprising that a much greater proportion of adults was present in distant-port areas than in near-port areas where juveniles and sub-adults usually occurred (fig. 7).

Rockfish species that exclusively inhabit shallower waters are probably better indicators than mixed-depth species of whether increased fishing effort in near-port areas affects local populations. Shallower water species generally have smaller home-range sizes and are residential as adults. Tagging studies indicate little or no movement for shallow water benthic species such as gopher and brown rockfishes (Larson 1980a; Matthews 1990; Lea et al. 1999). Shallow water nonbenthic species such as blue and olive rockfish also show very little movement, and the high degree of site fidelity may make these species susceptible to exploitation (Miller and Geibel 1973; Hartmann 1987; Jorgensen et al. 2007). This has been documented for olive rockfish in heavily fished regions in southern California (Love 1980), and trends of lower catch rates and smaller-sized fish for near-port areas for olive rockfish were apparent in this study. Catch

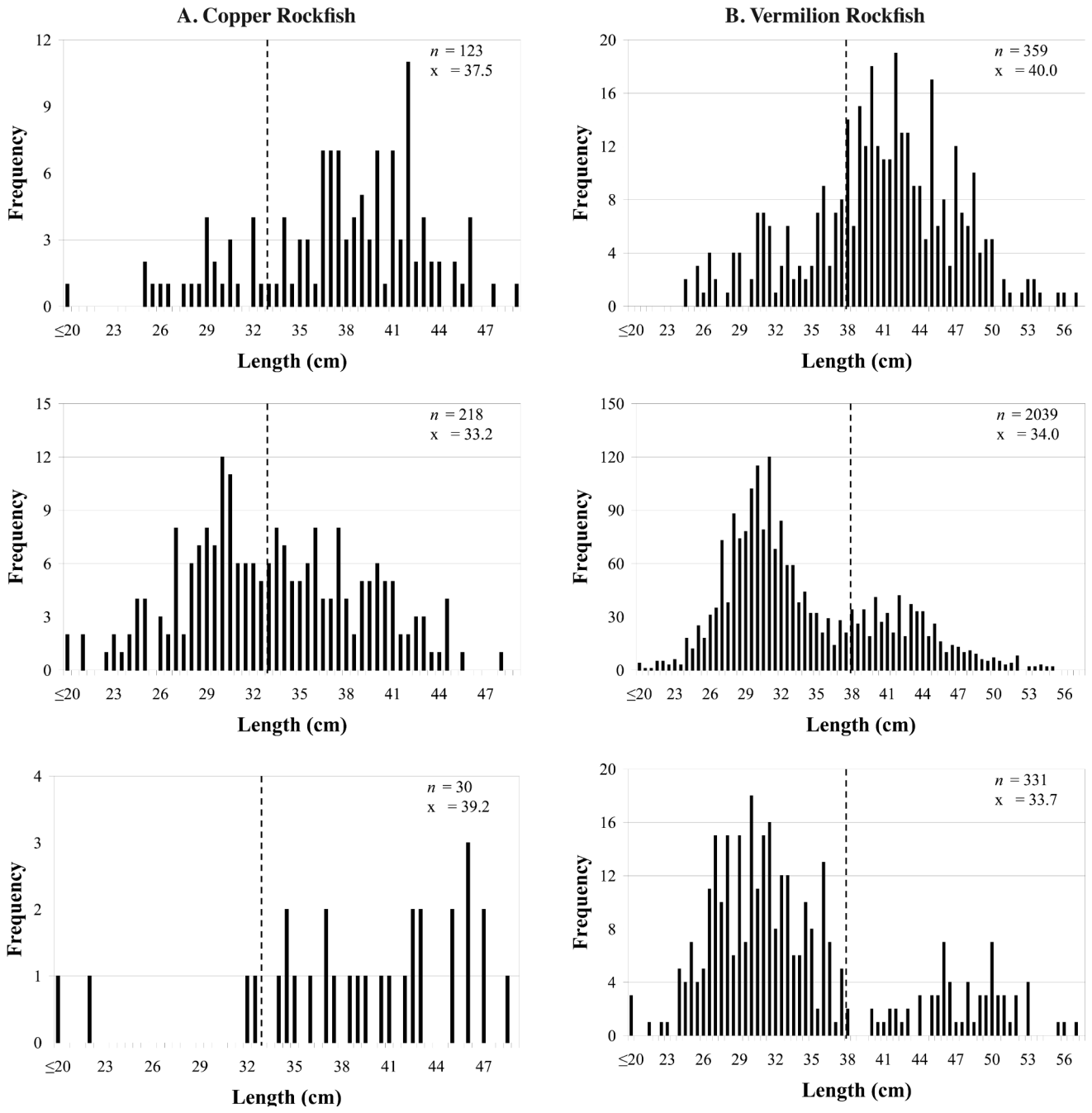

Figure 7 Length frequency histograms for fish sampled at San Simeon North (top), Near-Port (middle), and Pt. Sal/Purisima (bottom) areas in 2003-04. Sample size and mean length are given and vertical dashed line represents the size at 50% maturity.

rates for blue rockfish were not different between near and distant areas (except for Point Sal/Purisima), but there were larger-sized fish at San Simeon north compared to near-port areas (tab. 2). Even though there were proportionally larger-sized fish for the San Simeon area compared to near-port areas, both areas have a similar bimodal distribution with peaks of 25 and 32 cm corresponding to juvenile and adult size classes, respectively (fig. 8A). The presence of olive rockfish may indicate assemblage stress in near-port areas since their catch rates were lower. Also, size comparisons indicate that mostly adults reside in the San Simeon area while near-port areas had more juveniles than adults (fig. 8B).

Factors other than depth preferences may also have influenced the patterns observed for individual species from different areas, particularly habitat type. This espe-

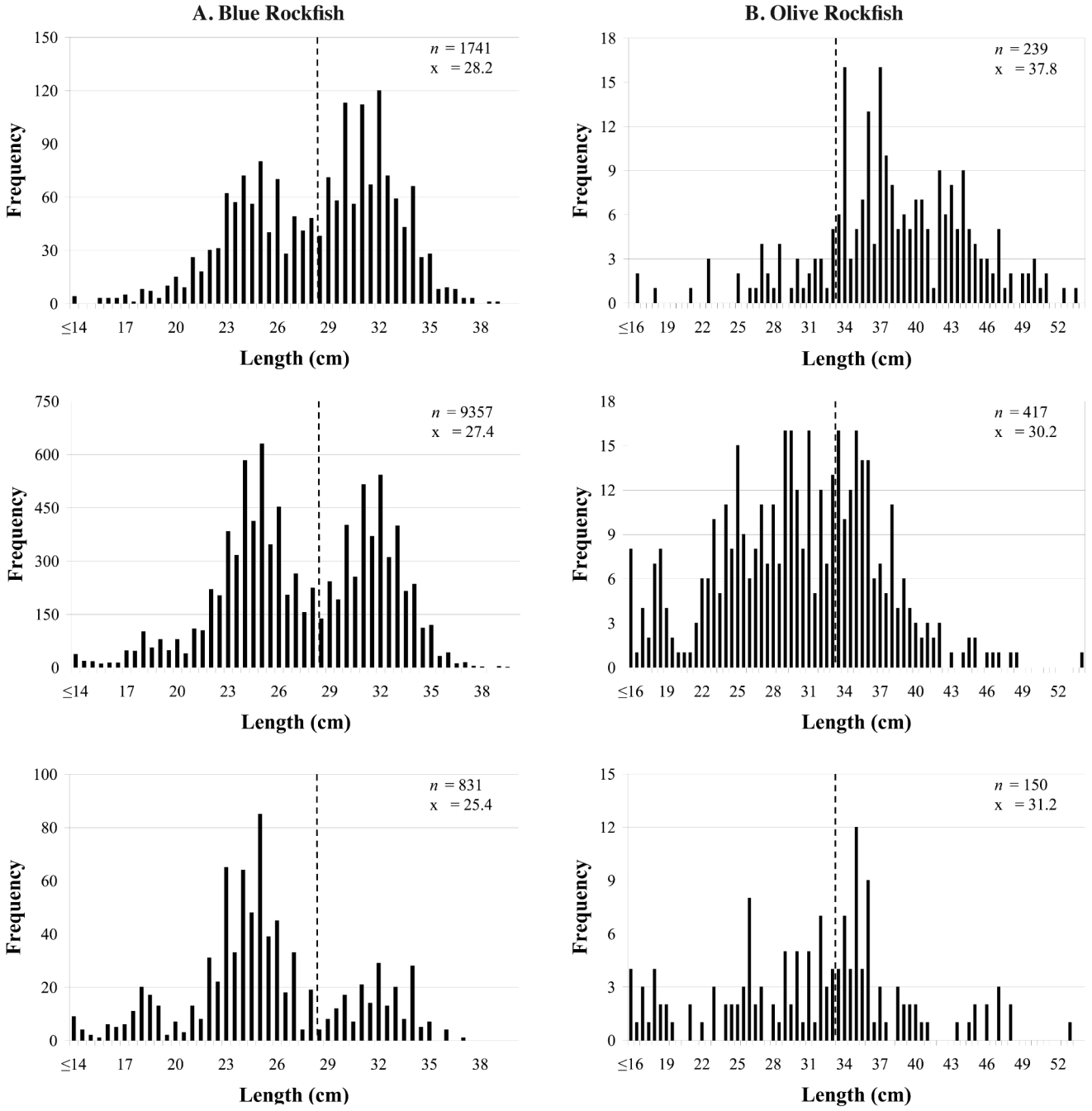

Figure 8 Length frequency histograms for fish sampled at San Simeon North (top), Near-Port (middle), and Pt. Sal/Purisima (bottom) areas in 2003-04. Sample size and mean length are given and vertical dashed line represents the size at 50% maturity.

cially seems to be the case with brown rockfish which were only abundant at the Point Sal/Purisima area. As mentioned earlier, brown rockfish typically occur in low-relief structures, such as cobblestone beds, which are found in the Point Sal/Purisima area. Blue and olive rockfish, however, are schooling and exclusively shallow-water species found over high-relief structures, which are found at the near- and distant-port areas for San Simeon. Gopher rockfish have a higher affinity for high-relief areas with much overgrowth (Larson 1980b). Since habitat and depth of capture were similar between near-port areas and San Simeon, it is not surprising that there were no gopher rockfish size differences between the two.

The results of this study have some general relevance to the establishment of Marine Protected Areas (MPAs), or "no-take" reserves, in central California in September

2007 (http://www.dfg.ca.gov/mlpa/ccmpas_list.asp#piedrassmca). Depending on the design and on the overall goal of any reserve, certain types of species groups may benefit while others may experience little effect (Carr and Reed 1993; Carr and Raimondi 1998). The no-take reserves in central California extend to depths of 20–40 fm (37–73 m), and the results from this study indicate that the species that would most likely benefit from this type of closure are those that exclusively inhabit shallow waters, such as blue, gopher, and olive rockfishes, since they do not move extensively. Marine reserves may also benefit species whose adults occur in both shallow and deep waters, such as copper and vermilion rockfish. However, this may be more difficult to discern since there is some degree of offshore movement towards deeper waters for these species. The species least likely to benefit from closure of shallow-water areas are those whose adults occur in deeper depths. Juvenile yellowtail and canary rockfish recruit to shallow-water areas and migrate to deep depths as adults. Hence, an MPA in shallow-water habitats is not likely to increase the density of adult fish in these areas. However, the closure of these areas may prevent growth overfishing and increase the proportion of juvenile fish that survive to adulthood.

Overall, the spatial and temporal patterns observed for the multi-species approach was mainly useful for elucidating habitat differences and their broad effect on species composition; it was secondarily useful in elucidating some climatically linked changes in relative abundance of species. The results from the multivariate analysis demonstrate that fishing does not appear to radically affect species composition by eradicating some heavily sought after or particularly sensitive species. The individual species trends mostly apply to shallow-water species. Thus, in examining differences in size or catch rates between heavily fished areas and those receiving less or no effort, species such as blue and olive rockfish would serve as good indicator species. Additionally, habitat differences and individual species preferences for specific habitats may have played a role in some of the differences in assemblages and CPUE between near- and distant-port areas, particularly with the Point Sal/Purisima area. This suggests that while CPUE was an effective measure for determining spatial and temporal patterns for fish assemblages, it should be used with caution for individual species and only under certain circumstances. To more effectively distinguish differences between near- and distant-port area assemblages, it would be beneficial to know the habitat type and species preferences for these habitats. A well-developed system has been established to classify seafloor habitats (Greene et al. 1999), but relatively few studies have examined benthic zones in detail in central California, with the exception of Yoklavich et al. (2002). Future studies might examine and characterize the benthic habitat along the SCC and determine whether rocky seafloor habitats in the area between Point Sal and Purisima Point are truly different from the rest of the SCC. Lastly, although patterns and trends in recreational rockfish catches within some areas of California such as the Southern California Bight are difficult to interpret due to shifts in fishing effort towards other species (i.e., yellowtail, barracuda, bonito, albacore, and kelp and barred sand basses) while fishing for rockfish (Love et al. 1998a; Dotson and Charter 2003), we can be sure that the trends examined in this study were exclusive to rockfishes and lingcod since albacore and salmon are caught on separate types of trips and were removed from the analysis for this study.

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AGE, GROWTH AND MATURITY OF JUMBO SQUID (*DOSIDICUS GIGAS* D'ORBIGNY, 1835) OFF THE WESTERN COAST OF THE BAJA CALIFORNIA PENINSULA

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ABSTRACT

Although jumbo squid (*Dosidicus gigas*) live off the western coast of Baja California, México, biological information for the species from this area is scarce. We processed the statoliths of 191 squid (144 females and 47 males) caught off western Baja California during 2004. The oldest male was 391 days old (mature at 690 mm dorsal mantle length, ML) and the oldest female was 433 days old (mature at 700 mm ML). Birth dates for both sexes were concentrated in January, indicative of a reproductive peak. Jumbo squid growth was best described by the logistic model. The largest females were larger (100 mm ML) and lived longer (1.4 months) than the largest males. The maximum daily growth rate in females was 2.09 mm per day (at 220 days; 407.6 mm ML) and in males was 2.1 mm per day (at 200 days; 365.9 mm ML). Finally, we conclude that squid from the Gulf of California grow faster than squid from off the western coast of Baja California.

INTRODUCTION

Jumbo squid (*Dosidicus gigas* d'Orbigny, 1835) is the largest and one of the most abundant species of the Ommastrephidae family and is distributed along the eastern Pacific Ocean from California (40°N) south to the southern part of Chile (45°S) (Nesis 1983; Nigmatullin et al. 2001). In México, the largest aggregations of jumbo squid occur in the Gulf of California and off the western coast of Baja California (Sato 1976; Klett-Traulsen 1996; Markaida and Sosa Nishizaki 2001).

In the Gulf of California, where a jumbo squid fishery has been established, this species has been widely studied (Klett 1982; Ehrhardt et al. 1983; Hernández-Herrera et al. 1998; Markaida et al. 2004). However, off the western coast of Baja California only exploratory studies have been conducted on the jumbo squid fishery (Sato 1976; Klett-Traulsen 1996). Recently the jumbo squid has greatly expanded its range in the eastern North Pacific Ocean and this may have important effects in the marine ecosystem (Field et al. 2007; Zeidberg and Robison 2007). The oceanographic and ecological conditions in the Gulf of California and off the western coast of Baja California differ, and such differences could influence the biological parameters (e.g., growth rate) of jumbo squid.

Currently, the jumbo squid fishery in the Gulf of California is regulated under the premise of a single cohort (Hernández-Herrera et al. 1998). However, some authors assert the existence of more than one cohort, which might imply more than one growth pattern (Ehrhardt et al. 1983; Nigmatullin et al. 2001; Markaida et al. 2004). Moreover, movements of jumbo squid within and outside the Gulf of California (Klett 1982; Ehrhardt et al. 1983; Markaida et al. 2005) are not considered in the current management strategy of the Mexican fishery.

The first works on squid age and growth were based in the modal frequency analysis (Hixon 1980; Ehrhardt et al. 1983; 1986). However, further studies have indicated that these analyses may not accurately predict length, because cephalopods, in general, have accelerated growth rates, large sizes, a short life span, partial spawning, and migratory behavior, which cause cohorts to overlap (Jackson and Choat 1992; Jackson et al. 2000). Since the 1980s, age and growth studies of squid have been performed using statolith growth increments from which individual age can be determined (Rodhouse and Hatfield 1990a).

Daily formation of growth increments in statoliths of *Dosidicus gigas* has not yet been confirmed, however, most studies that have validated age in other Ommastrephidae squid report a daily pattern (Dawe et al. 1985; Hurley et al. 1985; Lipiński 1986; Jackson et al. 1993; Lipiński et al. 1998). We thus assume that daily statolith increment deposition occurs in jumbo squid. Previous studies on jumbo squid aging through readings of statolith microstructure concluded that it lives between 1 and 2 years (Arkhipkin and Murzov 1986; Masuda et al. 1998; Markaida et al. 2004; Filauri 2005).

TABLE 1
Analysed statoliths from jumbo squid (*Dosidicus gigas*) caught off the western coast of Baja California, Mexico, during 2004.

Month	Both	Females	Males
January	67	56	11
April	15	11	4
July	41	32	9
October	68	45	23
Total	191	144	47

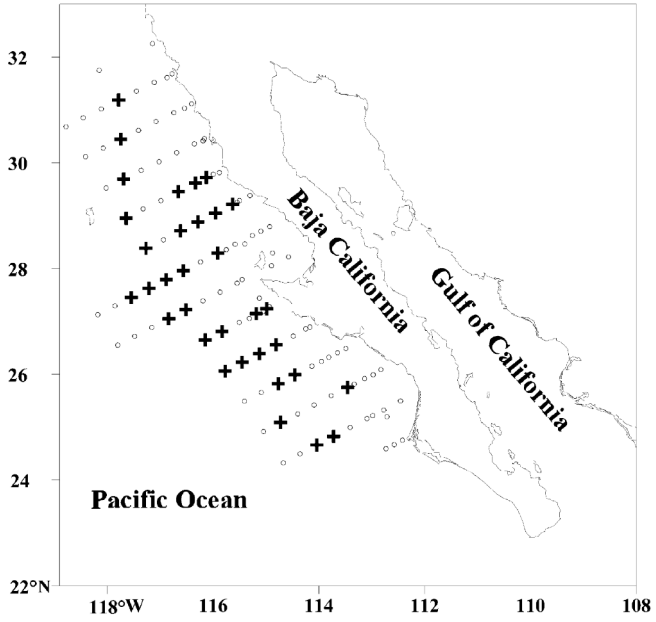

Figure 1. Grid sampling of oceanographic IMECOCAL cruises (circles) off western Baja California showing stations where jumbo squid (*Dosidicus gigas*) samples were caught in 2004 (crosses).

The aim of this work is to determinate the age and describe the growth of jumbo squid from the western coast of the Baja California peninsula using statolith increment counts.

MATERIALS AND METHODS

Jumbo squid were captured during four oceanographic cruises (tab. 1) off the western coast of Baja California during 2004 on board the BO *Francisco de Ulloa*. The cruises were developed within the IMECOCAL (Investigaciones Mexicanas de la Corriente de California http://imecocal.cicese.mx) program. The station network and the stations in which the analyzed specimens were captured are shown in Figure 1.

The squid were captured manually with jigs. Dorsal mantle length (ML) was measured to the nearest 5.0 mm. Sex was identified and reproductive condition evaluated according to the maturity scale of Lipiński and Underhill

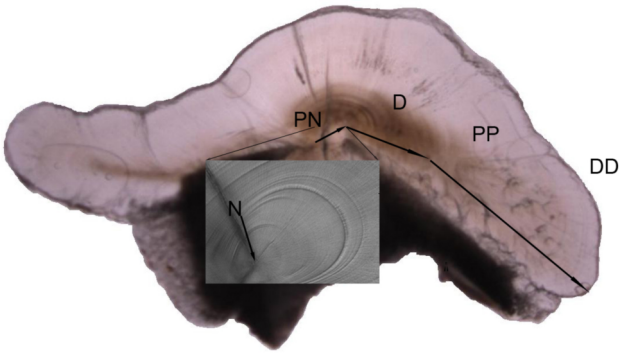

Figure 2. Growth zones in a jumbo squid (*Dosidicus gigas*) statolith between the nucleus (N) and the dorsal dome (DD): postnuclear (PN), dark (D), and peripheric (PP).

(1995): I-II (immature), III (maturing), IV-V (mature). Size-at-maturity groups were determined according to Nigmatullin et al. (2001): the small-sized group (males maturing at 130–260 mm ML, females at 140–340 mm ML), the medium-sized group (males maturing at 240–420 mm ML and females at 280–600 mm ML) and the large-sized group (males maturing at >400–500 mm ML and females at >550–650 mm ML). Squid heads were kept frozen until they were processed in the laboratory where statoliths were extracted and stored in 95% alcohol (Rodhouse and Hatfield 1990a).

Statolith length (SL), the distance between the extreme parts of the dorsal dome and the rostrum, was measured to within 1.0 μm (Arkhipkin and Murzov 1986) using an image analysis system and Image Pro Plus (Version 4.5.29) software. Statoliths were mounted on microscopic slides, ground (1000–1500 grit waterproof sandpaper), and polished (0.3 μm alumina powder) on both sides. The ground statolith was then embedded in Canada balsam under a coverslip and left to dry overnight at 70°C, according to the Arkhipkin method (Dawe and Natsukari 1991).

Two readers conducted the statolith increment counts independently using an optical microscope with a polarized light filter at 40×. The number of increments for each growth zone, postnuclear, dark and peripheric, were counted from the nucleus up to the border of the dorsal dome of the statolith (fig. 2; Arkhipkin and Perez 1998). The age of each squid was calculated as the average of both reader counts. When the difference between counts was >10% the statoliths were read again until a consensus was reached (Pierce et al. 2001).

The utility of the statolith in describing the jumbo squid growth pattern was evaluated by fitting a linear regression of SL to ML data for each sex. Six growth models were fitted to age-ML data (Markaida et al. 2004) for each sex. The model with the largest coefficient of determination (r^2) and the least coefficient of variance

(CV) in estimated parameters was chosen to describe growth (Arkhipkin et al. 2000).

Comparisons among selected growth curves per sex were performed by an F test (Arkhipkin et al. 2000):

$$F = \frac{\left[\frac{(SS_t - SS_p)}{(m+1)(k-1)}\right]}{\left[\frac{SS_p}{DF_p}\right]}, \quad (1)$$

$$DF_p = \sum_{t=1}^{k} n_t - k(m+1), \quad (2)$$

where $(m+1)(k-1)$ and DF_p are the degrees of freedom, SS_t is the total residual sum of squares, SS_p is the pooled residual sum of squares for k compared regressions, m is the number of variables to estimate (two for the curves considered here), and DF_p is the pooled degrees of freedom.

Absolute daily growth rates (DGRs, mm) were calculated for each 20-day interval by sex (Arkhipkin and Mikheev 1992):

$$\mathrm{DGR} = \frac{ML_2 - ML_1}{\Delta T}, \quad (3)$$

where ML_1 and ML_2 are the calculated MLs at the beginning and the end of each interval of time (ΔT = 20 days).

Jumbo squid hatching dates were obtained by subtracting the age from the date of capture (Campana and Jones, 1992). Squid were grouped by month and sex.

RESULTS

A total of 207 pairs of statoliths from 154 females and 53 males were collected. Statoliths were readable for 144 females and 47 males (tab. 1), which represented 92% and 87%, respectively, of the total sample. The size distribution of females indicated that at medium sizes (240–340 mm ML), they were mostly immature with a few maturing, and at large sizes (620–820 mm ML) were maturing and mature. Maturing and mature males were distributed into two size groups: medium (220–320 mm ML) and large (520–680 mm ML) (fig. 3).

The SL and ML relationship was highly significant ($r^2 = 0.89$, $p < 0.001$), indicating that growth is proportional in both variables and justifying the use of statoliths for describing the growth in ML of jumbo squid.

No significant differences were detected in the number of growth increments between the left and right statolith ($\chi^2 = 19.17$; d.f. = 20; $p > 0.05$), which validates using either statolith. Consequently, the right statolith was used in this study and, when not readable, the left was used.

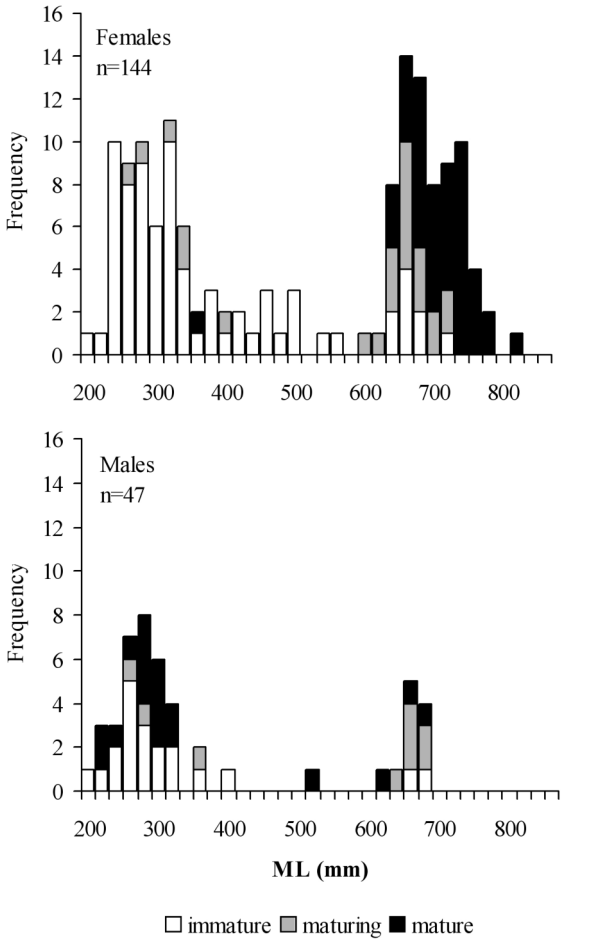

Figure 3. Mantle length (ML) frequency distribution by maturity stage and sex for jumbo squid (*Dosidicus gigas*) caught off the western coast of Baja California during 2004.

Age

The youngest male was 125 days old (at 210 mm ML) and immature; the oldest male was 391 days old, and was mature at 690 mm ML. The youngest female was 105 days old (at 240 mm ML) and immature; the oldest female was 433 days old (at 700 mm ML) and mature; and the largest female (830 mm ML) was 425 days old and mature.

Growth

The model that best fit age-ML data was the logistic model for both sexes ($r^2 = 0.98$, CV% 3.15 for females; $r^2 = 0.97$, CV% 7.4 for males) (fig. 4). The difference between the growth curves of both sexes was highly significant ($F_{3,182} = 2.25$, $p < 0.001$) (tab. 2). The asymptotic MLs calculated by the model were $Y\infty = 877.5$ mm ML for females and $Y\infty = 792.1$ mm ML for males.

TABLE 2
Statistical comparison of jumbo squid (*Docidicus gigas*) growth curves between sex and areas, western coast of BC (WC) 2004 and Gulf of California (GC) 1995–1997, from the logistic growth model. *n* = number of squid; RSS = residual sum of squares; RMS = residual mean square. Data are from Markaida et al. (2004).

	n	RSS	RMS	*F*	*p*
WC					
Females	142	1255.39	8.90	$F_{3,182}$ =	$p < 0.001$
Males	46	328.49	7.46	2.2591	
Females					
WC	142	1255.39	8.90	$F_{3,383}$ =	$p < 0.001$
GC	247	489250	2005	51.50	
Males					
WC	46	328.49	7.46	$F_{3,173}$ =	$p < 0.001$
GC	133	236077	1815	12.24	

Growth was larger for female jumbo squid; at 15 months old, females reached 767 mm ML and males 732 mm ML. Differences in growth between squid from the Gulf of California (Markaida et al. 2004) and from off the western coast of Baja California were highly significant for both sexes (tab. 2).

Age-size relationship at maturity

Squid from the medium size group were younger than squid from the large size group. Medium-sized females maturing and mature at 260–400 mm ML were 105 to 205 days old. Large females (>600 mm ML) were mostly mature at >350 days old (fig. 4). Medium-sized mature males (<400 mm ML) were <200 days old. Males from the large size group (>600 mm ML) were mostly maturing and >350 days old (fig. 4).

Growth rate

The daily growth rate (DGR) of ML (fig. 5) in young females (100 days) was 1.46 mm per day at 201 mm ML, while the maximum DGR (1.97 mm per day) was found in females 220 days old (409.4 mm ML). After this age, DGR decreased gradually to a minimum of 0.87 mm per day in squid 440 days old (758 mm ML). The DGR in young males (100 days old) was 1.57 mm per day at 181 mm ML. Maximum DGR for ML was 2.1 mm per day (at 200 days) at 365.9 mm ML; as squid aged, DGR decreased to a minimum of 0.59 mm per day (at 440 days and 726 mm ML). In general, jumbo squid from off the western coast of Baja California grow rapidly during the first 200 days, after which growth decreases gradually. Differences in growth by sex are evident when comparing DGR at similar ages; at 120 days, females grow slower (1.59 mm per day ML) than males (1.73 mm per day ML). The point of inflection in the DGR curve indicates that males reach their maximum growth rate before females. Finally, the decrease in DGR after the point of inflection is more accelerated in males (0.70 mm per day at 420 days) than in females (0.99 mm per day at 420 days).

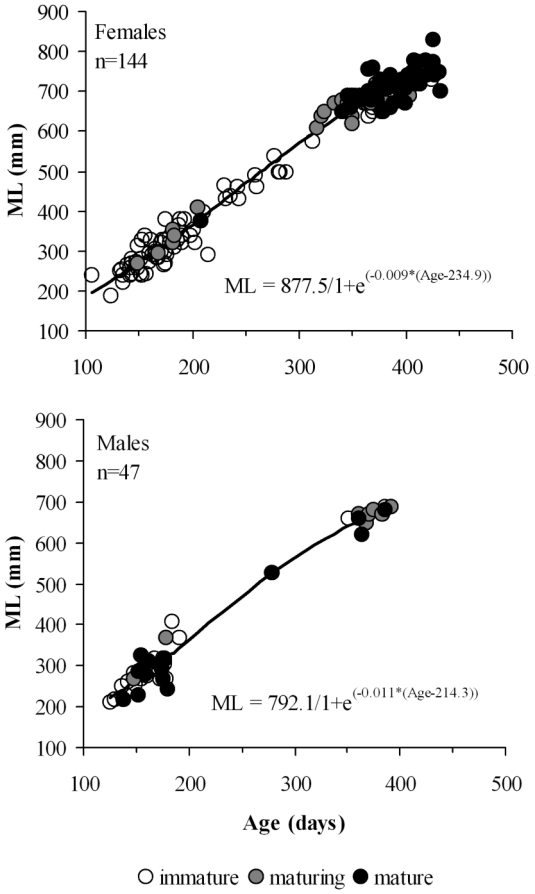

Figure 4. Relationship between age and mantle length (ML) and logistic growth curves for jumbo squid (*Dosidicus gigas*) caught off the western coast of Baja California during 2004.

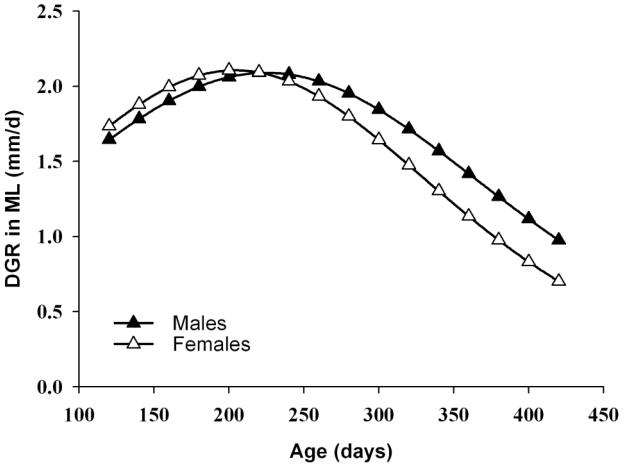

Figure 5. Daily growth rates (DGR) in mantle length (ML) (mm/d) of jumbo squid (*Dosidicus gigas*).

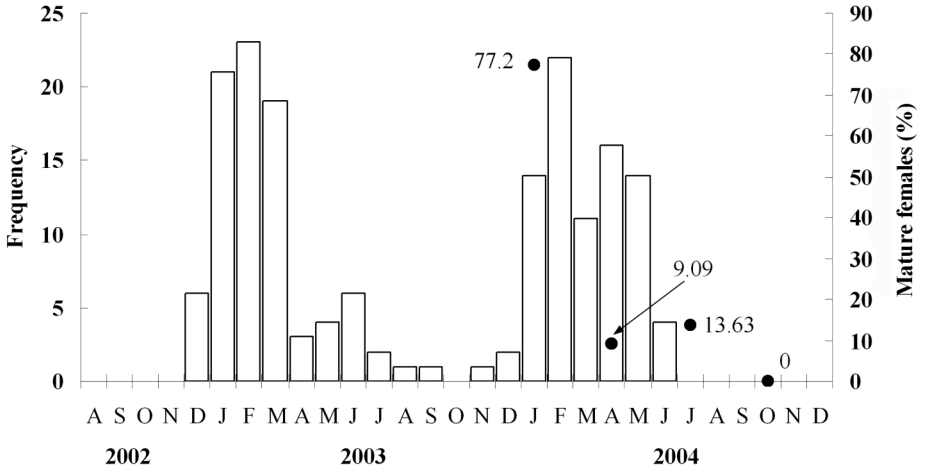

Figure 6. Monthly hatch date frequency distribution (bars, left axis) and percentages of mature female (dots, right axis) jumbo squid (*Dosidicus gigas*) caught off western coast of Baja California during 2004.

Hatching time

Jumbo squid hatch dates occurred from December 2002 to June 2004 and hatching modes occurred between January and March for 2003 and 2004 (fig. 6). In 2004, the hatching period extended to June. In January 2004, 77.2% of the females were mature which coincides with the beginning of the hatching season. Low mature female proportion in April 2004, however, did not correspond with the end of that hatching season.

DISCUSSION

Age

Maximum calculated ages from this study (433 days for females and 391 days for males) are similar to those in which jumbo squid between 1 and 1.5 years old were aged using statoliths (Arkhipkin and Murzov 1986; Masuda et al. 1998; Yatsu 2000; Markaida et al. 2004; Filauri 2005). In the Gulf of California, Markaida et al. (2004) found maximum ages of 442 days for females and 372 for males, similar to Filauri (2005) with ages of 450 and 385 days, respectively.

Growth

Accelerated growth and a short life span (0.5–2 years) are characteristic of most cephalopods. Growth differs between sexes, year, geographic area, and ontogenetic stage (Rodhouse and Hatfield 1990b; Yatsu 2000; Boyle and Rodhouse 2005). Factors which influence growth are: high rate of food consumption with a high capacity of converting energy into somatic growth (Boyle and Rodhouse 2005), a high temperature which accelerates growth rate, and migratory activity that limits potential energy for growth.

Different models have been used to describe subadult and adult jumbo squid growth, such as the von Bertalanffy in-size modal-distribution analysis (Ehrhardt et al. 1982; 1986), lineal (Masuda et al. 1998; Yatsu 2000), exponential, including juveniles (Arkhipkin and Murzov 1986), and logistic models (Markaida et al. 2004; Filauri 2005). The logistic model has also been used to describe the growth of other Ommastrephidae squid species (Arkhipkin and Silvanovich 1997; Arkhipkin et al. 1999; Arkhipkin et al. 2000). This study, however, was limited by the lack of intermediate-sized males (400–600 mm ML) to adequately complete their growth curve.

Comparison of growth curves

Males of the squid family Ommastrephidae start maturing before females, leading to a differential growth between sexes; thus females reach larger sizes (Arkhipkin and Murzov 1986; Rodhouse and Hatfield 1990b; Arkhipkin 2004; Markaida et al. 2004). Masuda et al. (1998), however, found statistically sexual differences in growth in only one out of three seasons analyzed.

Squid born in different seasons and areas experience different conditions, such as temperature and food availability, which influence their growth and can lead to temporal and spatial differentiations (Arkhipkin et al. 2000; Arkhipkin 2004). In squid from the Gulf of California (Markaida et al. 2004) and from off the western coast of Baja California, the growth rate differed between sexes. Squid from the Gulf of California, regardless of sex, grow more rapidly than squid from off western Baja California. Arkhipkin et al. (2000) also found differences in growth of the squid *Illex coindetii* from two different areas. Differences in growth in squid born during different seasons have also been observed, supporting our hypothesis that squid are influenced by seasonally oceanographic conditions (Masuda et al. 1998; Argüelles et al. 2001; Markaida et al. 2004). However, squid are a short-lived species sensitive to spatial and temporal vari-

ations. Therefore, the differences in growth we found between samples from the Gulf of California and off western Baja California collected with nearly a decade of separation may be an artifact of environment, year, etc., rather than due to location.

Growth rate

Growth rate is the proportion of increase in weight or length during an interval of time, and varies according to corporal dimensions (size or weight), age, sex, season, number of cohorts, geographic area, and hatching year (Arkhipkin and Perez 1998; Boyle and Rodhouse 2005). DGRs calculated for jumbo squid from the Gulf of California using statolith analysis range from 2 to 2.65 mm per day ML for squid 84 to 386 days old (108 mm to 875 mm ML) (Markaida et al. 2004) and from 1.47 to 2.26 mm per day ML for squid 158 to 450 days old (230 to 910 mm ML) (Filauri 2005). Both estimates are higher than our DGRs for squid of similar ages from off the western coast of Baja California (0.99–2.10 mm per day). Maximum DGRs for squid from the Gulf of California were 2.65 mm per day ML (230–250 days) in females and 2.44 mm per day ML (210–230 days) in males (Markaida et al. 2004). Thus, squid from the Gulf of California grow at a faster rate than those caught off western Baja California. However, jumbo squid tagging and recapture experiments in the Gulf of California yielded smaller DGRs of 1.0–1.5 mm per day at 500–700 mm ML (Markaida et al. 2005). This suggests that the longevity estimates given above might be underestimated.

In general, jumbo squid have higher growth rates than other squid of the Ommastrephidae family: 0.3–1 mm per day ML for *Illex illecebrosus* (Arkhipkin and Fetisov 2000), and 0.8–0.9 mm per day ML in *Todarodes pacificus* (Jackson and Choat 1992).

Hatching time

Counts of statolith growth increment allows hatching dates to be backcalculated. The presence of both a large number of hatching dates and a high proportion of mature individuals indicates massive spawning periods (Bigelow and Landgraf 1993). In the central Gulf of California multiple reproductive peaks have been identified for jumbo squid using modal distribution analysis (Ehrhardt et al. 1983; 1986; Klett-Traulsen 1996; Hernández-Herrera et al. 1998). Statolith analysis work in the same area did not identify reproductive peaks and suggests that jumbo squid reproduce all year in the Gulf of California (Markaida et al. 2004; Filauri 2005). In this study, we identified a hatching season of January–March for 2003 and 2004. While the sampling of only four months in a year limits our assumptions, this seasonality agrees with the reproductive peak described by Ehrhardt et al. (1983) in winter off the southwestern coast of Baja California.

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